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A Systematic Study of Recent Bison, with Particular Consideration of the Wood Bison (*Bison bison athabascae* Rhoads 1898)

C.G. van Zyll de Jong

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A SYSTEMATIC STUDY OF RECENT BISON, WITH PARTICULAR CONSIDERATION OF THE WOOD BISON (*BISON BISON ATHABASCAE* RHOADS 1898)

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Table of abbreviations used in this text

ACETW	Width of pelvis at acetabulum (see Fig. 2)
AMNH	American Museum of Natural History, New York City
AP	Allard-Pablo herd (see p. 2)
AOW	Anterior orbital width at notch (see Fig. 1)
BCPM	British Columbia Provincial Museum, Victoria
BM (NH)	British Museum (Natural History), London
BZM	Zoologisches Museum der Humboldt-Universität, Berlin
C7	Last cervical vertebra
CGP	Central Great Plains (see p. 3)
CHC	Circumference of horn-core at right angle to longitudinal axis (see Fig. 1)
CLLC	Core length on lower curve, tip to burr (see Fig. 1)
CLUC	Core length on upper curve, tip to burr (see Fig. 1)
CM	Carnegie Museum of Natural History, Pittsburg
CP	Canadian Prairies (see p. 3)
CRM	Canadian Rocky Mountains (see p. 3)
CVA	Canonical Variates Analysis
CW	Width of condyles (see Fig. 1)
CWS	Canadian Wildlife Service
D	Mahalanobis distance
DMNHC	Denver Museum of Natural History, Denver
DMNHT	Dallas Museum of Natural History, Dallas
DW	Diastema width (see Fig. 1)
EUS	Eastern United States (see p. 3)
FEML	Length of femur (see Fig. 2)
FEMW1	Proximal width of femur (see Fig. 2)
FEMW2	Distal width of femur (see Fig. 2)
FMNH	Field Museum of Natural History, Chicago
FP	Basilar length (see Fig. 1)
GPW	Greatest postorbital width (see Fig. 1)
GWA	Greatest width at auditory openings (see Fig. 1)
HB	Head-body length, not including tail
HCP	Height of the coronoid process (see Fig. 1)
HF	Length of hindfoot (see Fig. 3)
HUML	Length of humerus (see Fig. 2)
HUMW	Least width of humerus (see Fig. 2)
IH	Institut für Haustierkunde, Kiel
ILW	Width of the ilium (see Fig. 2)
ISCHW	Width at ischium (see Fig. 2)
ISUMZ	Iowa State University, Museum of Zoology, Iowa City
L 1-5	Lumbar vertebrae 1 to 5 (see Fig. 2)
LACM	Los Angeles County Museum of Natural History, Los Angeles
MCL	Length of metacarpal
MCW1	Proximal width of metacarpal
MCW2	Distal width of metacarpal
MCZ	Museum of Comparative Zoology (Harvard University), Cambridge, Massachusetts
MD	Mandibular depth (see Fig. 1)
MMMN	Manitoba Museum of Man and Nature, Winnipeg
M1M3L	M1-M3 alveolar length (see Fig. 1)
m1m3L	m1-m3 alveolar length (see Fig. 1)
MST	Minimum spanning tree
MTL	Length of metatarsal
MTW1	Proximal width of metatarsal (see Fig. 2)
MTW2	Distal width of metatarsal (see Fig. 2)
NDSU	North Dakota State University, Fargo
NR	Nyarling River herd (see p. 2)
NMC	National Museums of Canada, Ottawa
OC	Width of occipital constriction (see Fig. 1)
ON	Length occipital crest to naso-frontal suture (see Fig. 1)
PCA	Principal Components Analysis
PELV	Length of pelvis (see Fig. 2)
PL	Premolar length (pm2-ml) (see Fig. 2)
PMA	Provincial Museum of Alberta, Edmonton
Pm3AP	Posterior of m3 to posterior edge of articulating process (see Fig. 1)
Pm3F	Posterior of m3 to mandibular foramen (see Fig. 1)
P2M3L	P2-M3 alveolar length (see Fig. 1)

pm2m3L	Length of pm2-m3 (see Fig. 1)
PPHM	Panhandle-Plains Historical Museum, Canyon, Texas
PR	Peace River (see p. 3)
RADL	Length of radius (see Fig. 2)
RADW1	Proximal width of radius (see Fig. 2)
RADW2	Distal width of radius (see Fig. 2)
RHT	Rump height (see Fig. 3)
RW1 and RW2	Rostral width at maxillary — premaxillary suture (see Fig. 1)
SCAPL	Length of scapula (see Fig. 2)
SCAPW	Width of scapula (see Fig. 2)
SE	Snyder Expedition (see p. 2)
SGP	Southern Great Plains (see p. 3)
SHHT	Height of the shoulder (see Fig. 3)
SHTT	Spread of horn cores, tip-to-tip (see Fig. 1)
SMM	Science Museum of Minnesota, St. Paul
SMNH	Saskatchewan Museum of Natural History, Regina
SMP	Sanford Museum and Planetarium, Cherokee, Iowa
STL	Substitute total length (of mandible) (see Fig. 1)
T	Length of tail to last caudal vertebra (see Fig. 3)
T1-14	Thoracic vertebrae 1 to 14 (see Fig. 2)
TB	Length, tip of horn-core to upper base of burr (see Fig. 1)
TD	Transverse diameter of horn-core (see Fig. 1)
TIBL	Length of tibia (see Fig. 2)
TIBW1	Proximal width of tibia (see Fig. 2)
TIBW2	Distal width of tibia (see Fig. 2)
TL	Total length (see Fig. 3)
TMM	Texas Memorial Museum, University of Texas, Vertebrate Paleontology Lab, Austin
TTU	The Museum, Texas Tech University, Lubbock
UAMZ	University of Alberta, Museum of Zoology, Edmonton
UAMP	University of Alberta, Museum of Palaeontology, Edmonton
UCY	University of Calgary, Calgary
UM	University of Montana, Missoula
UPGMA	Unweighted pair group method using arithmetic averages
USGS	United States Geological Survey, Denver
USSC	University of Saskatchewan, Saskatoon Campus
USNM	United States National Museum, Washington
USRM	United States Rocky Mountains (see p. 3)
UWYO	University of Wyoming, Museum of Zoology, Laramie
VD	Vertical diameter of horn-core (see Fig. 1)
WAP	Width of articular process at mandibular notch (see Fig. 1)
WBNP	Wood Buffalo National Park (see p. 2)
WCP	Width of Coronoid process (see Fig. 2)
WHCO	Width of cranium between horn-cores and orbits (see Fig. 1)
WIEN	Naturhistorisches Museum, Wien
WMC	Width of mandibular condyle (see Fig. 1)
WMP	Width of skull at masseteric processes (see Fig. 1)
WR	Width of mandibular ramus (see Fig. 1)
WT	Body weight
YPM	Yale Peabody Museum, Yale University, New Haven
ZMA	Zoological Museum Amsterdam, Institute of Taxonomic Zoology, Amsterdam

Abstract

Multivariate morphometric analyses of cranial and post-cranial skeletal data from historical, Holocene, late Pleistocene and living remnant populations of bison were used to study geographic variation and subspeciation of Recent bison. Particular consideration was given to *Bison bison athabascae* and the taxonomic status of the remnant populations of presumed pure wood bison from the Nyarling herd. External characters (standard measurements, weight, outline shape and pelage characters) were compared in living forms.

Geographic variation in historic populations of the North American bison appears to have been clinal in nature over most of the distributional range in a predominantly south — north direction. However, a morphological discontinuity existed in the northwestern part of the range, coinciding approximately with the grassland — boreal forest ecotone. This phenotypic discontinuity between grassland and woodland populations fully justifies recognition of the two current subspecies *B. b. bison* and *B. b. athabascae*. The historical distribution of the two subspecies was reconstructed using information from specimens, historical reports and toponyms.

Comparisons of modern American and European bison with late Pleistocene — Holocene bison suggest, the existence of one variable chronospecies in the Holarctic region. The presence of bison closely similar to *B. b. occidentalis* and *B. b. athabascae* in eastern Siberia during the late Pleistocene-early Holocene demonstrates the existence of a Beringian population ancestral to living bison. It is probable that modern North American bison originated from the Beringian form and a southern form (*B. b. antiquus*). Subsequent evolution, coinciding with the expansion of the grasslands gave rise to *B. b. bison*. *B. b. bison* is the more derived of the current subspecies, whereas *B. b. athabascae* retains more of the ancestral characters, resembling *B. b. occidentalis* to a greater degree. Comparisons of cranial and, post-cranial elements, as well as those of external characters show that the Nyarling River bison are close to the original *B. b. athabascae*. However, the evidence also suggests that some gene flow between this herd and hybrid herds elsewhere in Wood Buffalo National Park did occur.

Résumé

Des analyses morphométriques multivariables de données crâniennes et squelettiques provenant d'échantillons de spécimens de bisons datant de l'Holocène et du Pléistocène, ainsi que de populations reliques ont été entreprises afin de clarifier des problèmes relatifs à la variation géographique et à la sous-spéciation des bisons contemporains.

On a considéré en particulier le *Bison bison athabascae* et la position taxinomique des bisons des forêts présumés pures qui ont survécu dans la région du fleuve Nyarling. Des caractères externes (mensurations types, poids, contour du corps et pelage) ont été comparés chez les formes vivantes.

La variation géographique chez les populations historiques de l'Amérique du Nord était apparemment clinale dans la plus grande partie de l'aire de répartition, surtout dans une direction nord-sud. Cependant une discontinuité morphologique existait dans la région du nord-ouest, adjacente à l'écotone entre la steppe et la forêt boréale. Cette discontinuité phénotypique entre les populations des steppes et de la forêt justifie les sous-espèces actuelles *B. b. bison* et *B. b. athabascae*. La répartition historique des deux sous-espèces a été reconstruite en utilisant les endroits où les spécimens ont été trouvés, des mentions historiques et des toponymes.

Des comparaisons entre les bisons actuels d'Amérique et de l'Europe et des bisons de la fin du Pléistocène ou du début de l'Holocène sugèrent qu'il y avait une espèce variable dans la région holarctique. L'existence d'un bison proche de *B. b. occidentalis* et de *B. b. athabascae* en Sibérie orientale vers la fin du Pléistocène ou le début de l'Holocène démontre qu'il y avait une population ancestrale du bison actuel en Béringie.

Le bison actuel d'Amérique du Nord a probablement eu comme ancêtre cette forme béringienne ainsi qu'une forme méridionale (*B. b. antiquus*). L'évolution durant l'expansion des steppes, a plus tard donné naissance au *B. b. bison*. Ce dernier est le plus évolué des sous-espèces actuelles, tandis que le *B. b. athabascae* a conservé plus de caractéristiques ancestrales plus marquées et ressemble plus au *B. b. occidentalis*. Une comparaison des caractéristiques squelettiques et externes démontre que le bison du fleuve Nyarling est proche de *B. b. athabascae* originaire de cette région. Les données indiquent en outre qu'il y avait un échange de gènes entre ce troupeau et les autres troupeaux hybrides, ailleurs dans le parc national de Wood Buffalo.

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The impetus for this study came from N.S. Novakowski. His close association with the rediscovery of the wood bison and the subsequent program to save it are widely known. His long standing interest in and knowledge of bison made him aware of the need for a full evaluation of the taxonomic status of the Nyarling herd. H.W. Reynolds, bison biologist with the Canadian Wildlife Service, gave much of his time and energies to ensure the success of this study, particularly by facilitating the salvaging of specimens. Without his help this study could not have been done. D.M. Shackleton of the University of British Columbia and H. Bohlken of the Institut für Haustierkunde in Kiel generously provided data from prairie bison and wisent respectively. I am grateful to Marla Weston, who provided me with the skull measurements of an east Siberian bison.

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Anne Macey assisted with data compilation, preliminary analysis and bibliography during the early phases of the study. D.B. Campbell measured and prepared specimens in the field and the laboratory, assisted by M. Laplante. I am grateful to my colleague D. McAllister, Curator, Ichthyology Section, for his assistance and the use of his computing facilities in analyzing the data. The line drawings, maps and graphs, which contribute so much to the value of the study are the work of Donna Naughton, who also contributed to the study in many other ways by gathering and compiling data and bibliographic references. W.A. Fuller, C.R. Harington, Marla Weston, and H.W. Reynolds made helpful comments on the manuscript.

Introduction

More than half a century ago, 6673 plains bison (*Bison bison bison*) were introduced to Wood Buffalo National Park, the range of the last surviving 1500 to 2000 wood bison (*B. b. athabascae*) (Seibert, 1925). Since then, it has been generally assumed that the wood bison had disappeared as a distinct subspecies as a result of interbreeding with the more numerous plains bison. The phenotype of the plains bison is now said to predominate in the Park (Fuller 1962). In 1957, however, an isolated herd of approximately 200 bison was discovered in the northwestern part of Wood Buffalo National Park, which was assumed to be a remnant of pure wood bison. This assumption was based on the observation that the intervening terrain, consisting of impassable and unsuitable habitat, formed a barrier to the movement of bison. Subsequent comparison of three specimens from this population with specimens of *B. b. athabascae* led to the conclusion that they were indeed wood bison (Banfield and Novakowski 1960). Shortly after the discovery of the remnant herd, the Canadian Wildlife Service undertook a program to save the herd from possible genetic inundation and to secure the survival of the subspecies (Reynolds 1979).

In the context of the Wood Bison Rehabilitation Program, the more extensive, in-depth analysis of the taxonomic status of the remnant herds of presumed pure wood bison was required, and the present study was undertaken to meet that need.

Although the emphasis in the present study is thus on *B. b. athabascae* and the identity and taxonomic status of the remnant herds of presumed wood bison, the analysis required the examination of the problem in the broader perspective of geographic variation and the systematics of historical bison populations and, to some extent, earlier forms of bison as well.

The near extermination of the bison in North America in the latter part of the nineteenth century precluded a comprehensive analysis of geographic variation in modern bison on this continent. The two North American subspecies recognized at present may therefore, not adequately reflect the geographic variation that once existed. It appears indeed likely that this species with its vast historical distribution may have had more distinct geographic forms than are now recognized. Some authors (Heck 1936, Mohr 1952, Krumbiegel 1980) have suggested, chiefly on the basis of historical illustrations and photographs, that the plains bison comprised at least two distinct geographic forms.

The recognition of the existence of a distinct form of bison in northern Canada can be traced back to the latter part of the last century (Allen 1876, Seton 1886) and culminated in the formal description of the subspecies *B. b. athabascae* by Rhoads. Rhoads' (1897) description was based on a single specimen which was not examined directly by him. The lack of a clear and unambiguous concept of the subspecies, resulting from the lack of critical comparisons, caused widely varying opinions on the taxonomic status of *B. b. athabascae* to persist to our day. Soper (1941: p.375) summed up the situation succinctly when he wrote: "Some regard the differences [between wood and plains bison] as but slight and of little significance at most a superficial divergence springing from environment; others again support Rhoads in this definite separation; while a third group leans to recognition of its status as a distinct species."

While a majority of mammalogists has subscribed to the view that *athabascae* is at least subspecifically distinct (e.g. Allen 1876, Seton 1886, Rhoads 1897, Rowan 1929, Skinner and Kaisen 1947, McDonald 1981), there have always been dissenters. For example, Hornaday (1889), Graham (1923) and Garretson (1938) would fit in Soper's first group, while Flerov (1979) represents a recent proponent of the third.

The lack of first hand knowledge of the living animal-only Seton and Rowan among zoologists could claim to have seen the plains and wood bison alive — and the small number of specimens available for study were undoubtedly at the root of this diversity of opinions. Quantitative analyses of *B. b. athabascae* museum material, primarily crania, were not undertaken until 1947 by Skinner and Kaisen and 1978 by McDonald. The ill-conceived introduction of the plains bison into the last refuge of the wood bison apparently doomed the latter's survival as a distinct subspecies before a detailed study of all aspects of this bison could have begun. The historic discovery in 1957 raised the hope that not all was lost. The aim of the present study is to determine to what extent the remnant saved represents the original wood bison that once roamed the area of what is now Wood Buffalo National Park.

The principal questions addressed in the present study are:

1. What was the extent and nature of geographic variation in North American Recent bison?
2. What are the morphometric relationships of historical North American forms to earlier Holocene and the late Pleistocene forms, and what are the implications for the origin of Recent bison?
3. How are recent New and Old World bison related?
4. What is the taxonomic status of present remnant herds in Canada?

The first three of these questions have been addressed before. This study is, therefore, chiefly a reassessment, using a somewhat different approach and different analyses. An analysis of the evolution of bison since the early Pleistocene lies outside the scope of the present study. For a current treatment of this subject see Weston, Shackleton and Harington's (in preparation) comprehensive analysis of fossil and recent material from Eurasia and North America. In the context of the present study, it suffices to glance back to the earlier Holocene and late Pleistocene in order to gain some insight into the possible origin of contemporary forms of bison.

The fourth question focuses on the survival of the wood bison as a distinct subspecies. Aside from its scientific interest, the answer to this question may have practical implications for bison conservation and management.

The effects of interbreeding of the plains and wood bison on the phenotypic variation of the present herds in Wood Buffalo National Park could, unfortunately, not be fully assessed in the present study because of a lack of specimens. Further work on this population will be undertaken.

Materials and Methods

The analyses in this study are based on data derived from 528 skulls; 143 mandibles; 36 postcranial skeletons; a smaller number of skins as well as on external measurements and weights of fresh carcases and information on external characters from live animals gathered in the course of this study.

Pertinent information on the specimens used and number of specimens in each sample are given in Appendix 1.

The specimens were divided *a priori* for purposes of analysis into a number of subsamples, on the basis of sex, geographic origin and era as follows:

Subsamples Representing Living Remnant Populations.

Subsample 1. Descendants of the Allard-Pablo herd (AP). This sample consists chiefly of specimens from Elk Island National Park, with smaller numbers of specimens from Wainwright (former Buffalo National Park) and Riding Mountain National Park.

Subsample 2. Wood Buffalo National Park (WBNP), consisting of specimens collected 20 years or more after the final release of AP stock and presumed to represent the mixed descendants of it and *athabascae*. Only an inadequate sample of mainly immature animals could be gathered, precluding a complete analysis of this population.

Subsample 3. Snyder Expedition (SE). This small sample consists of specimens collected in Wood Buffalo National Park in 1934–35 (Goodwin 1935). The aim of the expedition was to collect specimens of wood bison for the American Museum of Natural History and the National Museum of Canada. Selection was on the basis of external appearance by implication, but as these animals were collected 6 or 7 years after the last introduction of plains bison into the park and none of the collectors had prior first-hand knowledge of pure *B. b. athabascae*, the taxonomic identity of these specimens is in doubt. Because of the definite bias used in selecting the specimens, this sample cannot be used to represent the hybrid population in Wood Buffalo National Park as McDonald (1978, 1981) has done.

Subsample 4. Nyarling River herd (NR), a sample comprising specimens of presumed pure *B. b. athabascae* discovered in 1957 and their descendants. Small numbers of animals transferred from this herd to other areas (18 animals to the Mackenzie Bison Sanctuary in 1963 and 23 animals to Elk Island National Park in 1965) (Reynolds 1979), formed the foundation of all present wood bison herds.

Subsample 5. *bonasus*, a sample representing the European bison (*B. b. bonasus* and a few *B. b. caucasicus*) and consisting chiefly of craniometric data made available by Dr. H. Bohlken.

Subsamples Representing Historical Populations

Subsample 6. *athabascae*, consisting of specimens of *B. b. athabascae* collected prior to the 1925–28 introductions of plains bison to Wood Buffalo National Park, or those collected during or shortly after that period, that could be unequivocally assigned to *B. b. athabascae* on the basis of age. The bulk of the 6673 plains bison introduced consisted of yearlings (72.3%) and two-year-olds (22.7%) the remainder of three-year-olds (Soper 1941). Only one true *B. b. athabascae* female specimen (NMC 10405) was available for study. McDonald's (1978, 1981) rejection of this specimen as a true *B. b. athabascae* appears to be without foundation. The female's age was determined on the basis of the number of incremental lines in her tooth cementum as 10+ years. As she was collected in March 1928, she was therefore at least 7 years old when the first introductions were made in 1925.

Subsample 7. Canadian Prairies (CP) consists of specimens representing the original historical population of bison from the Canadian prairie provinces.

Subsample 8. Canadian Rocky Mountains (CRM), a sample consisting of historical specimens, surface and near-surface finds, from Banff, Jasper and Waterton Lakes National Parks.

Subsample 9. Peace River region (PR) consisting of skulls and partial skulls of historical specimens from the Aspen-parklands of the Peace River region of Alberta and British Columbia. This area is of particular interest with regard to the historical distribution and geographic variation of bison. As there were few specimens from this area in collections, a publicity campaign was mounted through local newspapers to solicit information about specimens picked up locally and in private ownership. In this manner additional specimens from the area were located and examined.

Subsample 10. Central Great Plains (CGP) consisting of specimens representing historical populations from the central Great Plains in the United States, including specimens from Iowa, Kansas, Montana, Nebraska, South Dakota and eastern Wyoming.

Subsample 11. United States Rocky Mountain (USRM), consisting of historical specimens from the Rocky Mountains and areas to the west, including specimens from Colorado, Montana, western Wyoming, and Oregon.

Subsample 12. Southern Great Plains (SGP) consisting of specimens representing the historical population in Texas.

Subsample 13. Eastern United States (EUS) consisting of a small sample from Kentucky.

Subsamples Representing Earlier Holocene and Late Pleistocene Populations

Subsample 14. *occidentalis* representing early to mid-Holocene North American bison.

Subsample 15. *antiquus* representing late Pleistocene to Holocene North American bison.

Subsample 16. *priscus* representing late Pleistocene Beringian bison from Alaska.

In addition to the above samples data from individual skulls of Holocene or late Pleistocene bison were used (see Appendix 1).

The subsamples are referred to in the text by the taxonomic designations or the acronyms listed above. Cranial measurements were in some instances partially (CGP; USRM: *occidentalis*), or wholly (SGP; EUS; *antiquus*; *priscus*) derived from McDonald (1978). For further information on specimens used see Appendix 1.

The cranial and mandibular measurements used are those of Skinner and Kaisen (1947), and Shackleton et al. (1975) with a few additional ones (see Figure 1). Post-cranial measurements and external measurements taken are shown in Figures 2 and 3 respectively. The abbreviations of the measurements used are listed in figures 1 to 3.

The numerical data were analyzed using univariate and multivariate methods. Basic statistics were calculated for all measurements and the significance of differences between sample means tested with Student's *t* test. Use of single variables for discriminating between subspecies or sexes was evaluated using the method of Lubischew (1962). Cranial, post-cranial and external variables were also subjected to principal component analysis (PCA) (in cases involving individual specimens) or canonical variates analysis (CVA) (of *a priori* group) and distance analysis (Blackith and Reyment 1971, Neff and Marcus 1980, Davies 1971). Conformity of the data to the assumptions of multivariate normality and equal variance covariance structure were not tested. According to Sokal and Sneath (1973: p. 127) ". . .considerable robustness to violation of these assumptions

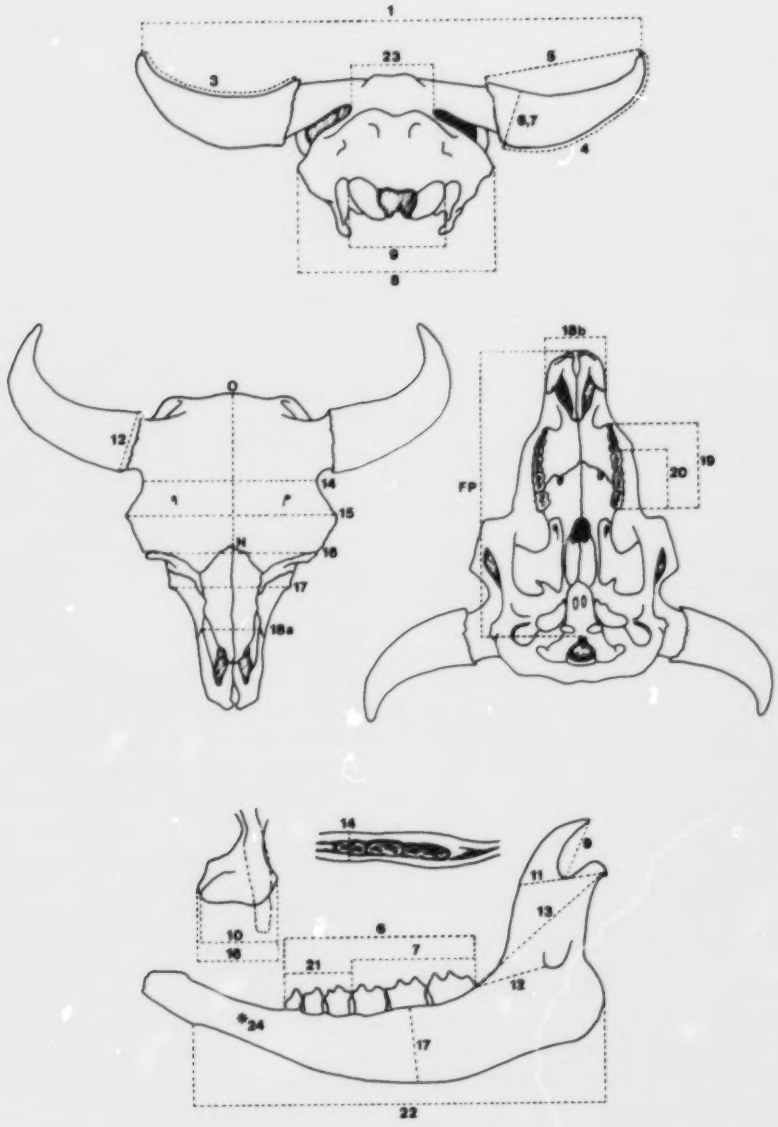


Figure 1. Cranial and mandibular measurements used. Numbers correspond to those of Skinner and Kaisen (1947) and Shackleton et al. (1975). Cranial measurements: 1) Spread of horn cores, tip–to–tip (SHTT); 3) Core length on upper curve, tip to burr (CLUC); 4) Core length on lower curve, tip to burr (CLLC); 5) Length, tip of core to upper base of burr (TB); 6) Vertical diameter of horn core at right angles to longitudinal axis (VD); 7) Circumference of horn-core at right angle to longitudinal axis (CHC); 8 Greatest width at auditory openings (GWA); 9) Width of condyles (CW); 12) transverse diameter of core at right angle to longitudinal axis (TD); 14) Width of cranium between horn-cores and orbits (WHCO); 15) Greatest postorbital width (GPW); 16) Anterior orbital width at notch (AOW); 17) Width of skull at masseteric processes above M1 (WMP); 18 a and b) Rostral width at maxillary-premaxillary suture (RW1, RW2); 19) P2–M3 alveolar length (P2M3L); 20) M1–M3 alveolar length (M1M3L); 23) Width of the occipital constriction (OC); FP basilar length; ON length occipital crest to nasofrontal suture. Mandibular measurements: 7) m1-m3, alveolar length (m1m3L); 9) height of the coronoid process (HCP); 10) Width of coronoid process (WCP); 11) Width of articulating process at mandibular notch (WAP); 12) Posterior of m3 to mandibular foramen (Pm3F); 13) Posterior of m3 to posterior edge of articulating process (Pm3AP); 14) Width of ramus at posterior of m1 (WR); 16) Width of mandibular condyle (WMC); 17) m2 alveolar to base height (mandibular depth) (MD); 21) pm2-m1 (premolar length) (PL); 22) substitute total length (STL); 24) diastema width (DW).

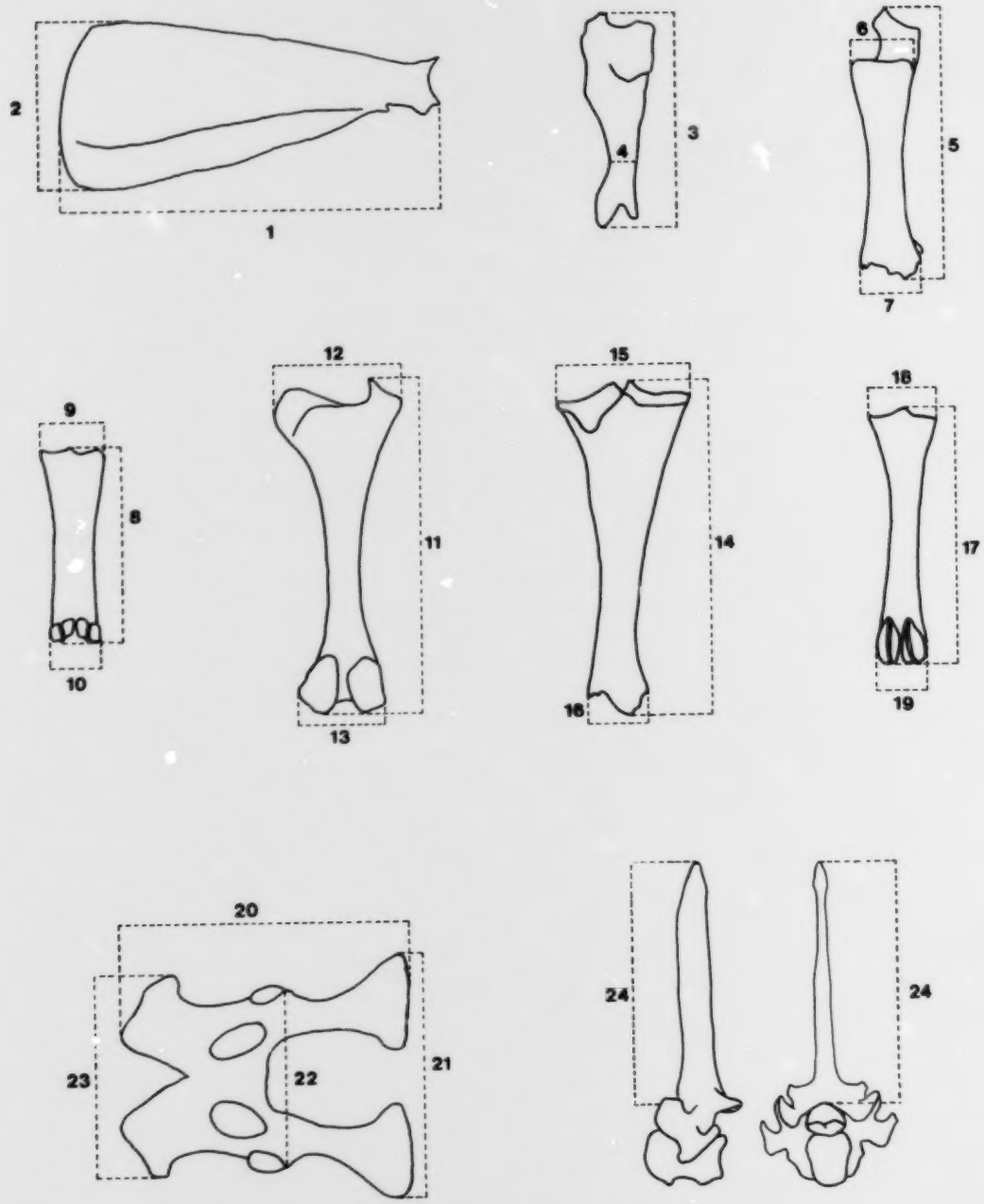


Figure 2. Measurements of the postcranial skeleton. 1) Length of scapula (SCAPL); 2) Width of scapula (SCAPW); 3) Length of humerus (HUML); 4) Least width of humerus (HUMW); 5) Length of radius (and ulna) (RADL); 6) Proximal width of radius (RADW1); 7) Distal width of radius (RADW2); 8) Length of metacarpal (MCL); 9) Proximal width of metacarpal (MCW1); 10) Distal width of metacarpal (MCW2); 11) Length of femur (FEML); 12) Proximal width of femur (FEMW1); 13) Distal width of femur (FEMW2); 14) Length of tibia (TIBL); 15) Proximal width of tibia (TIBW1); 16) Distal width of tibia (TIBW2); 17) Length of metatarsal (MTL); 18) Proximal width of metatarsal (MTW1); 19) Distal width of metatarsal (MTW2); 20) Length of pelvis (PELV); 21) Width of ilium (ILW); 22) Width at acetabulum (ACETW); 23) Width at ischium (ISCHW); 24) Length of neural spine of vertebrae, last cervical, thoracic, and lumbar (C7, T1-14, L1-5).

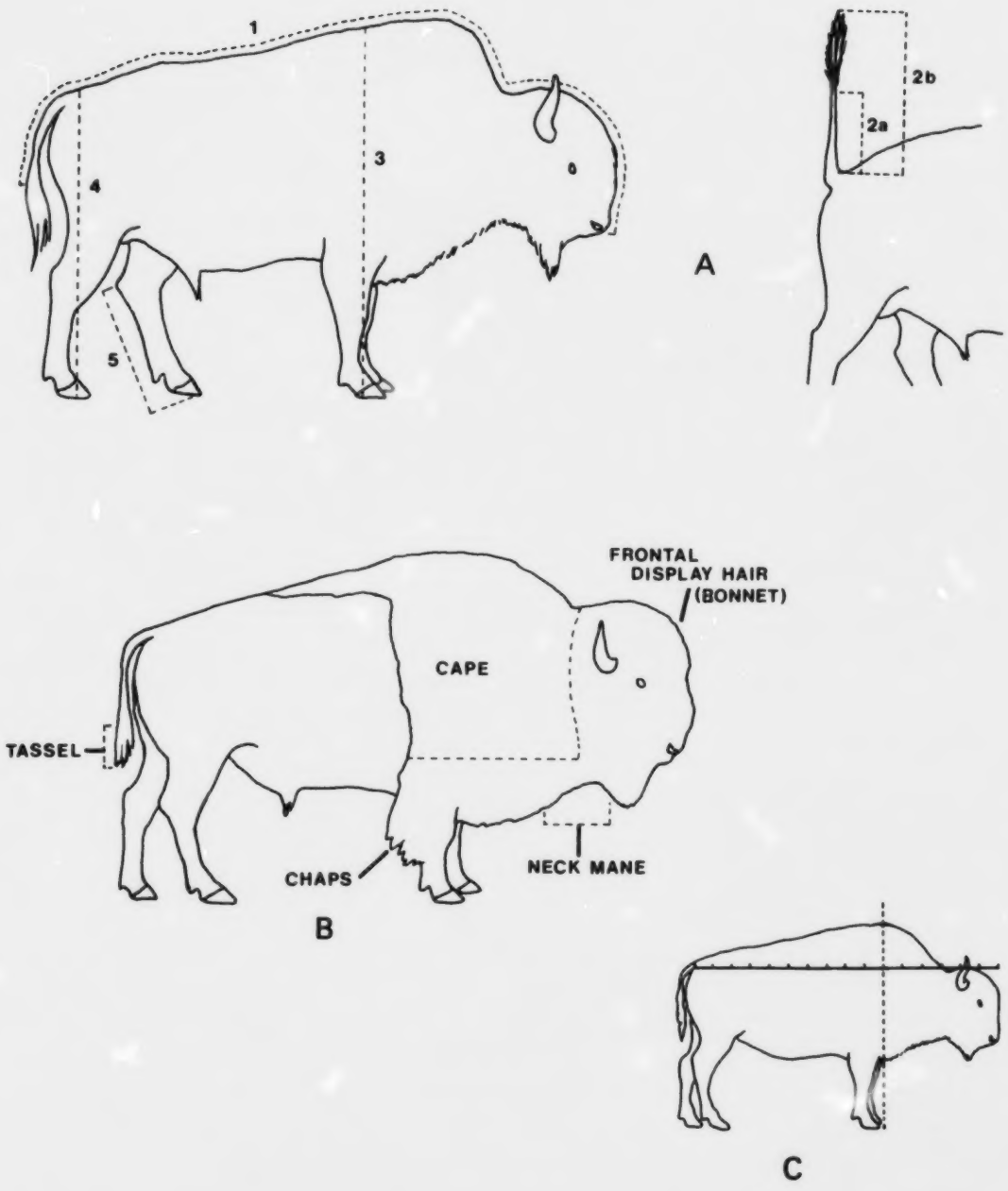


Figure 3. A. External measurements: 1) Total length (TL); 2) Length of the tail a) to last caudal vertebra (T); b) to end of tassel. 3) Height of the shoulder (SHHT); 4) Rump height (RHT); 5) Length of hindfoot (HF). B. Terminology used for pelage characters, the broken line outlines the area of the cape. C. Standardization for outline-shape analysis. The divisions on the horizontal axis are in centimeters.

has been demonstrated". Moreover the descriptive use of multivariate techniques ". . . as a data-analytic procedure . . . to ordinate and efficiently describe multivariate observations" (Albrecht 1980: p. 681) is valid. Discriminant function analysis (DFA) for two groups for use in assigning unknowns to *B. b. bison* or *B. b. athabascae* was also used (Appendix 2). Calculations were performed on a Hewlett-Packard 9831 A desk-top computer, using programs from Davies (1971) adapted by D. McAllister.

During preliminary analysis the initial number of cranial variables, 34 in all, was reduced to a smaller number (7 to 11) in subsequent analyses. Deletion of variables was based on redundancy reflected by high correlations between variables and poor representation of a variable in the *B. b. athabascae* sample in order to maximize sample size for this taxon. The initial number of mandibular variables (23) was likewise reduced to 15 in the final analyses.

In the craniometric analyses data from adult animals only were used. Assignment of skulls to age classes was based on the degree of fusion of the parietofrontal and frontal sutures in males (Shackleton *et al.* 1975) and toothwear in both sexes (Skinner and Kaisen 1947; Fuller 1959b; Frison and Reher 1970).

To elucidate the questions posed in the introduction the following analyses were undertaken:

1. The morphometric relationships of historical populations (subsamples 6–13) were assessed using CVA and distance analysis of craniometric data. CVA obtains a low dimensional display of the data and maximizes between group variation relative to within group variation (Campbell and Atchley 1981). Plots of the canonical variates scores in two and three dimensions were produced to display the scatter of individuals and the distance between group centroids. To assess the contribution of the original variables to the canonical variates the vectors scaled to have a length of two standard deviations were plotted on the graph (Jolicoeur 1959). The canonical variables were used to calculate a matrix of Mahalanobis distances (Pythagorean distance in standardized canonical variate space). To facilitate interpretation of the relationships among groups in three-dimensional canonical variate space and to reveal possible distortions of distances, minimum spanning trees (MST) (Sneath and Sokal 1973) were computed and projected on the graph. The distance (D) relationships among the samples were in some instances further summarized by a distance dendrogram derived by unweighted pair group cluster analysis (UPGMA) (Sneath and Sokal 1973) of the distance half-matrix.

The 11 cranial variables used in the analysis included 6 horn measurements, which showed high intra-locality correlations suggesting common epigenetic control and redundancy of information (Thorpe 1976). This set of variables was used, however, so that some of McDonald's (1978) data could be included in the analysis.

Different sets of variables, in which redundancy had been reduced by selecting those variables with low intra-locality correlations (Thorpe 1976), were used to analyze the morphometric relationships of northern populations CP, CGP, CRM, PR and *B. b. athabascae* further. To determine the extent of the historical distribution and area of possible intergradation of the two forms, all available specimens from critical areas, many being partial skulls, were used. Histograms of variables most frequently preserved in historical specimens were constructed (Figure 4) to aid in selecting combinations of characters useful in assigning unknown skulls to the correct taxon with a degree of probability. Discriminant function analysis, using combinations of these variables varying from 11 to as few as 3 were used to assign unknown specimens from critical areas (Appendix 2).

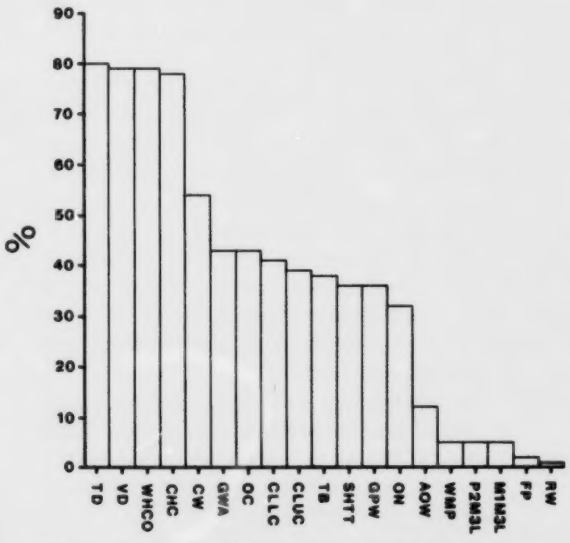


Figure 4. Histogram showing the frequency of intact measurable variables in old skulls found on or near the surface of localities in the historic range of the bison.

2. The morphometric relationships of Recent subspecies to earlier Holocene and late Pleistocene forms (*occidentalis*, *antiquus*, *priscus*) was analyzed in the same manner as that of the historical populations and by PCA.
3. The relationship of modern New and Old World bison was assessed by CVA of 11 cranial variables. A somewhat different set of cranial variables, corresponding to that of Bohiken (1967) was used.
4. The taxonomic status of living remnant herds in Canada was determined using CVA of craniometric data and PCA of postcranial variables and external measurements and weights. In addition, outline shape and pelage chracteristics of NR bison were compared with those of plains bison.

The PCA of post-cranial variables was done on the variance-covariance matrix and correlation matrix of the data. External measurements and weights were transformed into logarithms ($\log_{10}$) prior to PCA of the variance-covariance matrix of the data.

Differences in outline shape and pelage characters of American plains bison and European bison are well known and discussed in detail by Mohr (1939, 1952) and Flerov (1932), and summarized by Haltenorth (1963). Information on the external characteristics of the original *B. b. athabascae*, on the other hand, is poorly documented. Aside from a few museum skins, which give information on pelage characters, there is very little objective information on the external characteristics of *B. b. athabascae*. Early reports of eye witnesses appear to agree on two characters in which *B. b. athabascae* differed from *B. b. bison*, i.e. size (larger) and colour (darker). Existing photographs (e.g. Graham 1923, Kitto 1924) predating the 1925–28 introductions are generally inadequate for a detailed comparison of the two forms. In the absence of a *B. b. athabascae* reference sample for external characters, NR specimens were compared directly to AP specimens and to a lesser extent also to plains bison from different herds.

Outline tracings were obtained from photographs of bison in profile. Outlines were standardized so that each had an arbitrary length of 16 cm along a horizontal axis from the base of the tail to the plane of the nose (Figure 3). The two orthogonal axes superimposed on the outline allow for a quantitative comparison of differences in outline shape. Perpendicular distances of contour points (at intervals of 1 cm on the X axis) to these axes could thus be recorded and compared.

Pelage characters in NR and AP bison were compared using visual character analysis, comparison of frequencies of occurrence of certain characters and a character index (Mayr 1969). A number of characters which were found to differ in NR and AP samples after preliminary examination were subdivided and ranked into two or more character states, whose frequency of occurrence in each group could then be determined and compared. Characters showing the least amount of overlap were then assigned a numerical value, and could thus be used in a character index. The typical or prevailing character state of AP bison was designated as 1. The character state encountered in the NR sample most unlike that found in the AP sample was designated 0. Where intermediate character states are recognized they were assigned intermediate values (see Appendix 3). In interpreting the data it was assumed that character states most unlike those found in AP bison or absent in AP bison were characteristic of *B. b. athabascae*. Where possible, confirmation was sought from independent sources. With the addition of one outline shape character the character index was used to score individual animals to obtain an index of their position on an axis representing external phenotypic variation from *B. b. bison* (100%) to *B. b. athabascae* (0%).

Results

1. CVA of Craniometric Data from Historical Populations of North American Bison.

The results of the CVA and distance analysis of samples representing historical populations from different parts of the former distributional range based on 11 cranial variables are summarized in Figures 5, 6 and 7.

Examination of the three-dimensional graph (Figure 5) clearly shows the isolated position of the *athabascae* centroid relative to the other forms. The centroids for the populations, excluding *athabascae* which may be collectively referred to as plains bison, are separated by relatively small

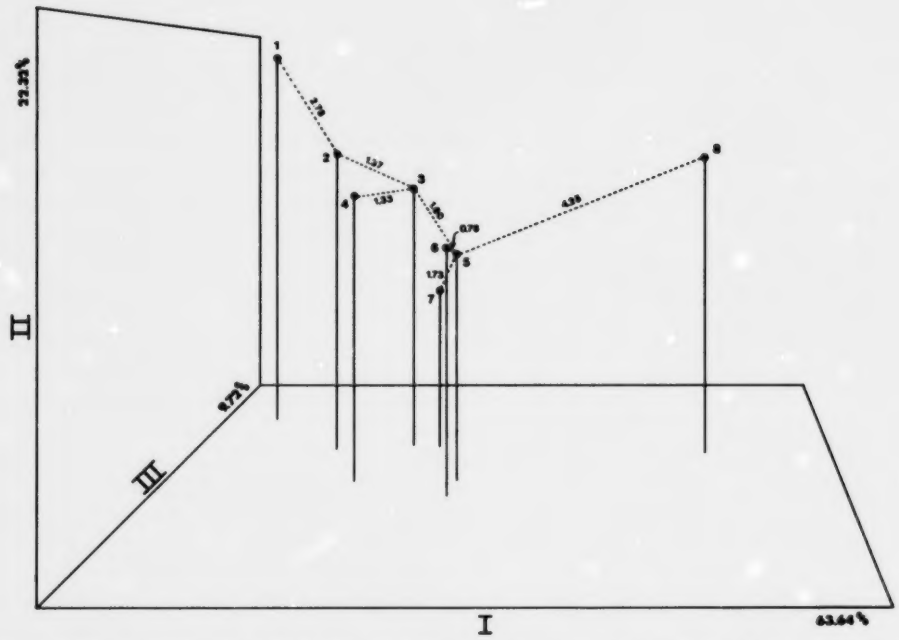


Figure 5. Projection of the centroids for eight samples of historical North American bison populations onto the first three canonical axes, based on six horn measurements and five cranial measurements. The centroids are connected by a minimum spanning tree. 1) Eastern U.S. 2) Southern Great Plains; 3) U.S. Rocky Mountains; 4) Canadian Rocky Mountains; 5) Peace River area: 6) Canadian prairies; 7) Central Great Plains; 8) *B. b. athabascae*.

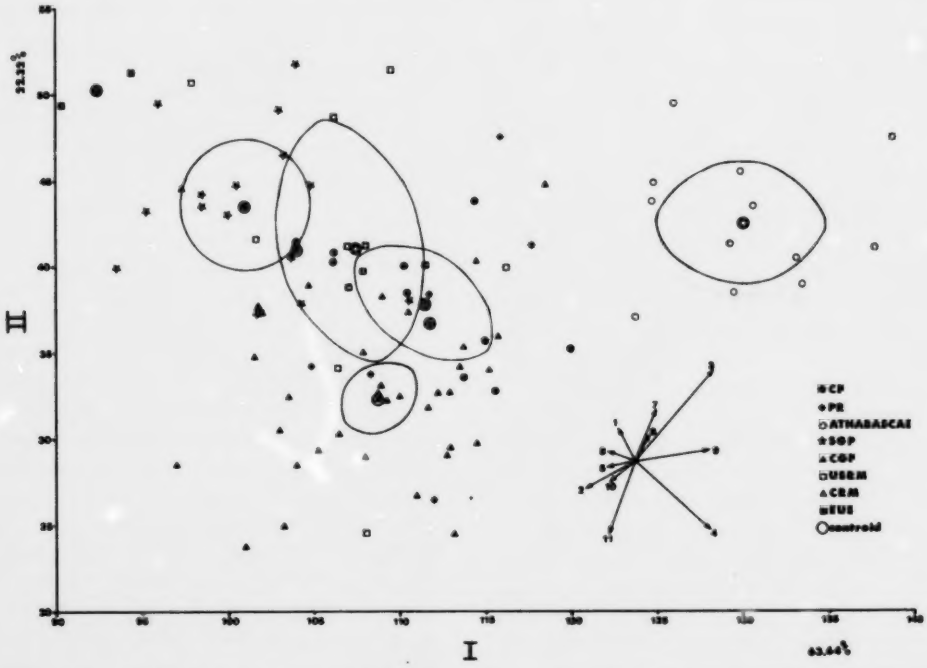


Figure 6. Projection of individual specimens and centroids of eight samples onto the first two canonical axes. The projection of character vectors shows the relative contribution of the original variables to the canonical variates. The vector lengths equal two standard deviations. The ellipses represent the 95% confidence region of the centroids. 1 ON; 2 VD; 3 TD; 4 GWA; 5 CW; 6 WHCO; 7 GPW; 8 SHTT; 9 CLUC; 10 TB; 11 CHC.

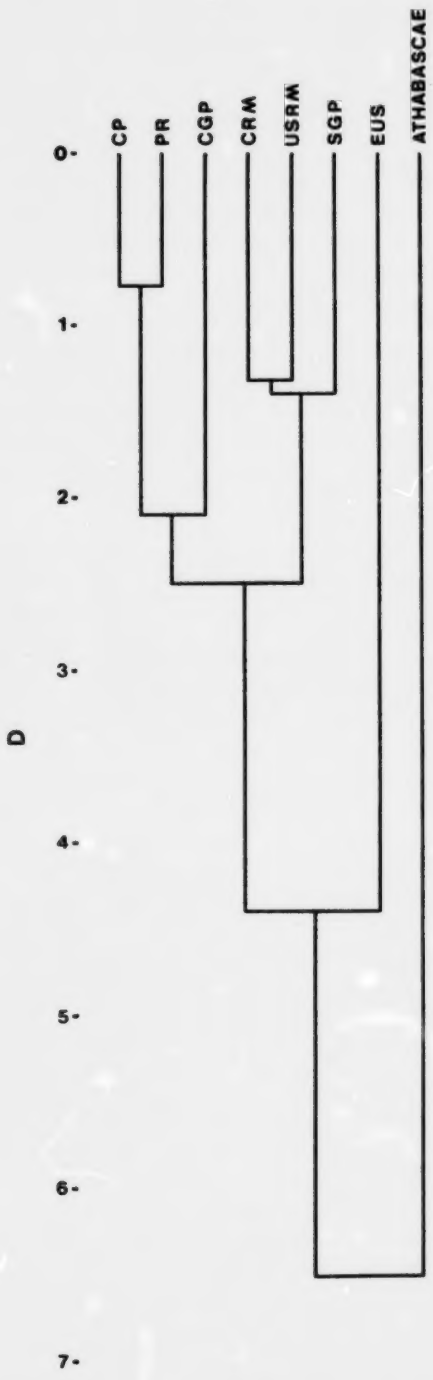


Figure 7. Dendrogram summarizing the generalized distances between historical populations of North American bison in canonical variate space (cf. Figure 5.) The cophenetic correlation coefficient is 0.87.

distances (D) from their nearest neighbors in canonical variate space as the MST shows. The distances linking the plains bison centroids vary from 0.76 (between CP and PR) to 2.78 (between EUS and SGP), whereas *athabascae* and its nearest neighbor PR are considerably more distant from each other (D = 4.25). In addition to their proximity to one another the centroids of the plains bison samples are distributed along a diagonal axis running from the left back upper corner down toward the center of the three-dimensional space. The centroid of *athabascae*, on the other hand, is situated well to the right of this axis. This axis represents clinal variation in the plains bison in an approximately north-south direction.

The projection of the canonical variates scores for individual specimens and their group centroids on the first and second canonical axes shows that the plains bison samples form a series of overlapping clusters (Figure 6). The clinal variation within the plains bison, referred to above, appears to be predominantly that of overall size (Table 1), with the smaller forms in the upper left corner and the larger ones lower down towards the center.

The relative contribution of the original variables to the canonical variates is shown by the vector diagram on the plot of canonical variates (Figure 6). The vector separating the plains bison centroids from each other is GWA (no. 4), a measurement significantly correlated ($r = 0.81$ $P < .02$) with overall size (expressed as the mean of means of all measurements for each group). The vector for GWA runs parallel to the axis of clinal variation in the plains bison suggesting that the variation is essentially one of size.

The *athabascae* cluster, on the other hand, does not overlap any of the plains bison clusters and is clearly divergent from the axis of clinal variation of the plains bison. The position of *athabascae* suggests a difference in shape of the *athabascae* crania compared to those of plains bison. The character vectors (Figure 6) indicate that *athabascae* differs from the plains bison sample in having greater TD, CLUC, GPW, WHCO. The distance relationship of the historical populations is shown in Figure 7. The distance dendrogram clearly shows the divergent position of *athabascae*.

The morphometric relationship of the northern plains bison (CP, CGP, USRM, CRM and PR) and *athabascae* was subjected to further analysis using different sets of variables, ranging from 11 to as few as 3, in order to elucidate variation in the grassland-boreal forest ecotone, the possible

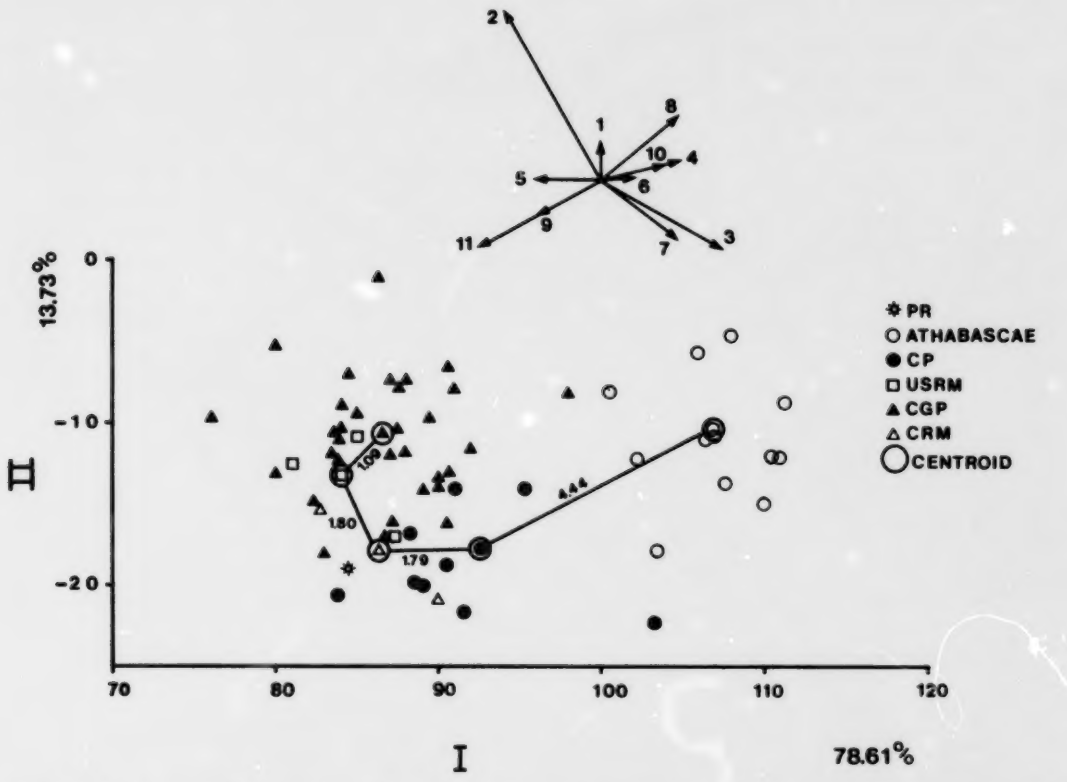


Figure 8. Projection onto the first two canonical axes of individual specimens and centroids (connected by a minimum spanning tree) of six samples representing populations of northern plains bison and wood bison. CVA is based on 9 cranial and 2 horn characters. Lengths of character vectors equal two standard deviations. 1 ON; 2 VD; 3 TD; 4 GWA; 5 CW; 6 WHCO; 7 GPW 8 P2M3L; 9 M1M3L; 10 OC; 11 WMP.

zone of intergradation between wood and plains bison.

The graph in Figure 8 summarizes the results of the CVA of 11 cranial variables, of which only two are horn measurements. The results are remarkably similar to the previous CVA of 11 variables in which horncore measurements predominated. There is a clear separation between northern plains bison samples and *athabascae*. One specimen from the Peace River parklands and two specimens from the Canadian Rocky Mountains were scored as unknowns and plotted to determine their affinities. All three specimens fell within the scatter of the plains bison samples (Figure 8). The character vectors show that *athabascae* differs from the plains bison samples mainly in greater GWA, TD and smaller WMP and CW.

A CVA using seven cranial variables with an increased number of specimens from the Peace River parklands produced a similar picture (Figure 9), but with smaller inter-centroid distances. The interesting result to note is the somewhat intermediate position of PR in relation to *athabascae* and the plains bison samples. Similar patterns were observed in CVA's using progressively fewer variables, with the main difference being the concomitant decrease of intercentroid distances and increasing overlap of clusters representing the geographic samples. As few as three variables still gave only approximately 4% overlap between *athabascae* and plains bison reference samples and could therefore be used in assigning unknown, geographically intermediate specimens — a large number of them with only a few measurable variables (Figure 4), to the nearest reference sample. Partial specimens from the area between the main distributional ranges of plains and wood bison could thus be identified and used in delineating the contact zone between wood and plains bison. The geographic and morphometric relationships based on three variables

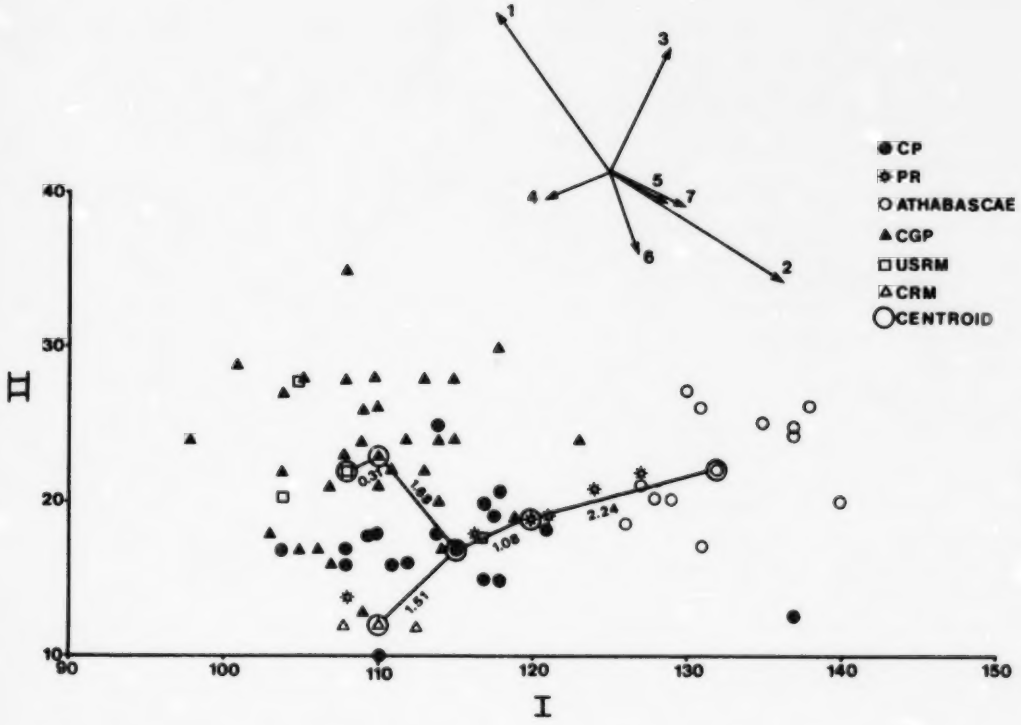


Figure 9. Morphometric relationship of northern plains bison and wood bison on the basis of a CVA of five cranial and two horn characters. 1 VD; 2 TD; 3 GWA; 4 CW; 5 WHCO; 6 GPW; 7 OC.

(VD, TD, WHCO) of four geographic samples (CP, CRM, PR, *athabascae*) are shown in Figure 10.

The use of three variables, although decreasing the discrimination, allowed most available specimens to be used in determining the area of contact or intergradation between plains and wood bison. The small number of measurements and decreased power of discrimination meant that large plains bison or small wood bison could be assigned incorrectly. For example a known large plains bison (NMC 8833) was scored as a wood bison based on the discriminant function using only three variables. However, a general trend and the affinities between geographic samples can be discerned from MST in Figure 10, with CRM and CP and PR and *athabascae* respectively being relatively close, while the two pairs are more distant from each other. It appears likely that the zone of contact was situated somewhere midway between CP and PR, judging from the relative proportions of *bison* and *athabascae* scores in the area. About 23% of the PR specimens scored on the bison side of the dividing point, compared to about 50% of specimens from the boreal forest and aspen parklands section of Alberta separating the Peace River parklands from the grasslands. Compared to the CVA using 7 variables and fewer specimens the most notable difference in the three variable analysis is the shift of the PR centroid to *athabascae*. The proximity of some PR specimens to CP suggests that the populations in the two areas were at least in occasional contact.

2. CVA of Craniometric Data from Recent European and North American Bison.

The morphometric relationship of crania of modern North American (historical samples) and European bison are shown in Figure 11. Prairie bison and European bison are separated from each other by the smallest distance. The main separation between the two forms is along the second axis, with the most important contribution to discrimination coming from OC, AOW (greater in *bonasus*) and GWA, WMP, GPW (greater in *bison*). Discrimination between *athabascae* and the other two taxa is chiefly along the first axis with

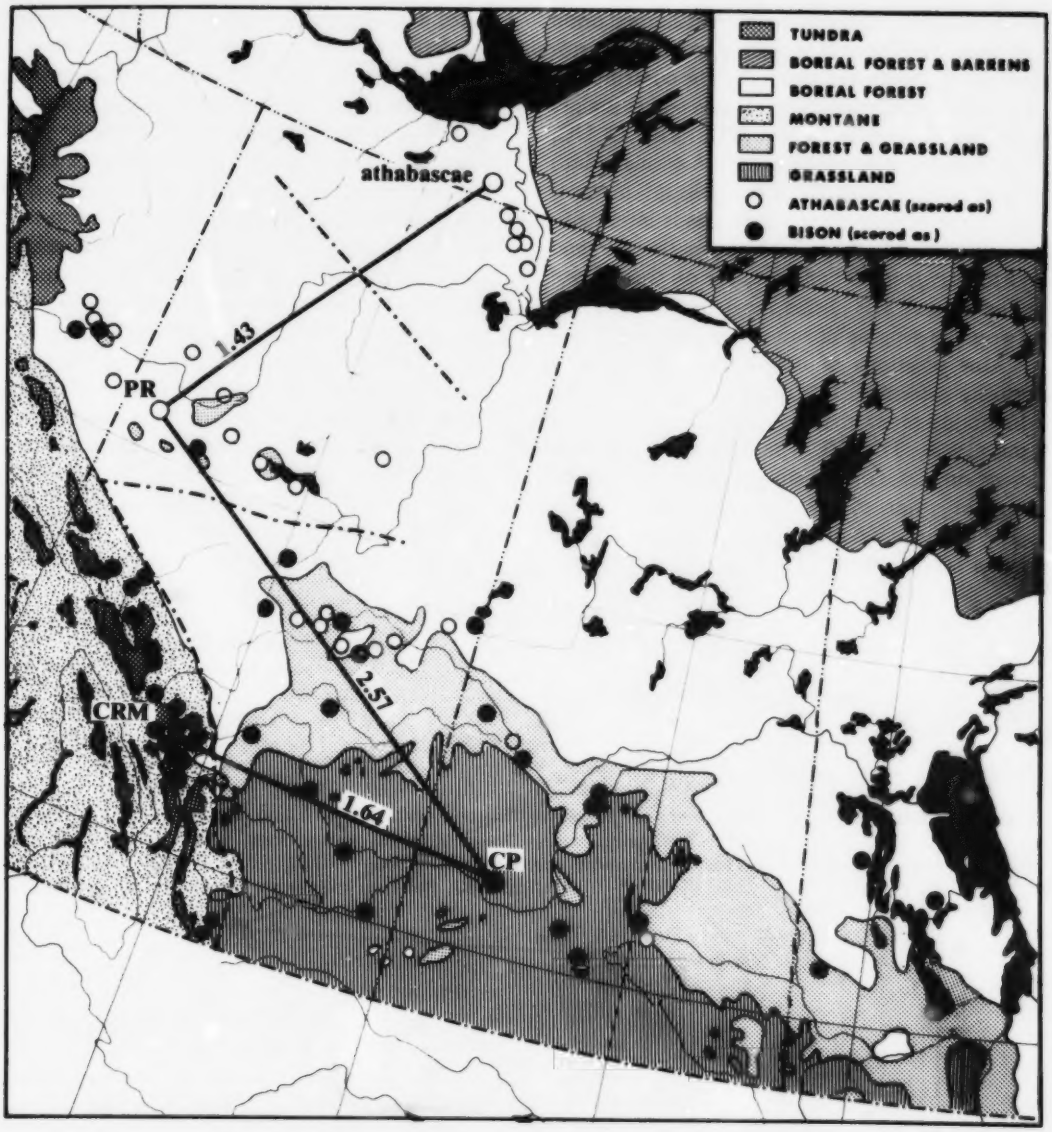


Figure 10. Morphometric relationship of contiguous populations of bison from the Canadian prairies (CP), the Rocky Mountains (CRM), the Peace River area (PR) and from the area of what is now Wood Buffalo National Park (*athabascae*), based on three cranial characters. Solid dots represent specimens with values on the *B. b. bison* side of the mid point between the *B. b. bison* and *B. b. athabascae* centroid scores, hollow circles those with values on the *athabascae* side. The distances between groups show their mutual relationship and indicate that the most change occurs between CP and PR. Present vegetation zones are based on Rowe (1972).

the greatest distance being that between *athabascae* and *bonasus*. Contribution to the discrimination between *athabascae* and *bonasus* comes mainly from GWA, GPW, FP (greater in *athabascae*) and AOW, OC. Discrimination between *athabascae* and *bison* is contributed to mainly by GWA, GPW, FP and WMP (Figure 11).

3. Multivariate Craniometric Comparisons of Historical, Holocene and Late Pleistocene Bison.

The results of the CVA of 11 cranial variables of historical, and early to mid-Holocene (*occidentalis*, *antiquus*) and late Pleistocene forms from Alaska (*priscus*) are shown in Figure 12. The sepa-

ration between smaller modern short-horned bison and larger long-horned Holocene and late Pleistocene bison is along the first axis. The contribution to the discrimination along this axis comes mainly from horn measurements (TD, TB, CLUC, SHTT) and to a lesser extent from cranial width measurements (WHCO), (cf. Table 1) The position of *athabascae* on the first axis is intermediate with respect to the plains bison on the one hand and to *occidentalis* and *antiquus* on the other.

The second axis shows most of the variation between the geographic samples of historical bison with the positions of *athabascae* and EUS on opposite extremes. The contribution to the discrimination along the second axis comes mainly from GWA, TD, TB. The high score of *athabascae* on this axis is owing in large part to the large dimension of GWA in this form.

The distance relationships of the centroids are summarized by the MST in Figure 12 and the distance dendrogram in Figure 13. Examination of the latter clearly shows the remote position of *priscus* from the others, the intermediate position of *athabascae* between modern plains bison and *occidentalis* and *antiquus*, and, within the plains bison the relatively distant position of EUS.

A well preserved skull of a bison from eastern Siberia (Moscow Paleontological Museum 835–624–39), believed to be of late Pleistocene or early Holocene age (Sher 1971), is of particular interest for the evolutionary history of Recent bison. This specimen was scored and the values obtained were plotted in the canonical variate space in Figure 12, to compare its position relative to that of Nearctic bison. The position of the east Siberian specimen, as one can see, is intermediate between *athabascae* (D = 2.85) and *occidentalis* (D = 3.23), suggesting a close affinity between these three forms.

Crania of northern plains bison (CP, CGP, USRM, CRM) and *athabascae* were further com-

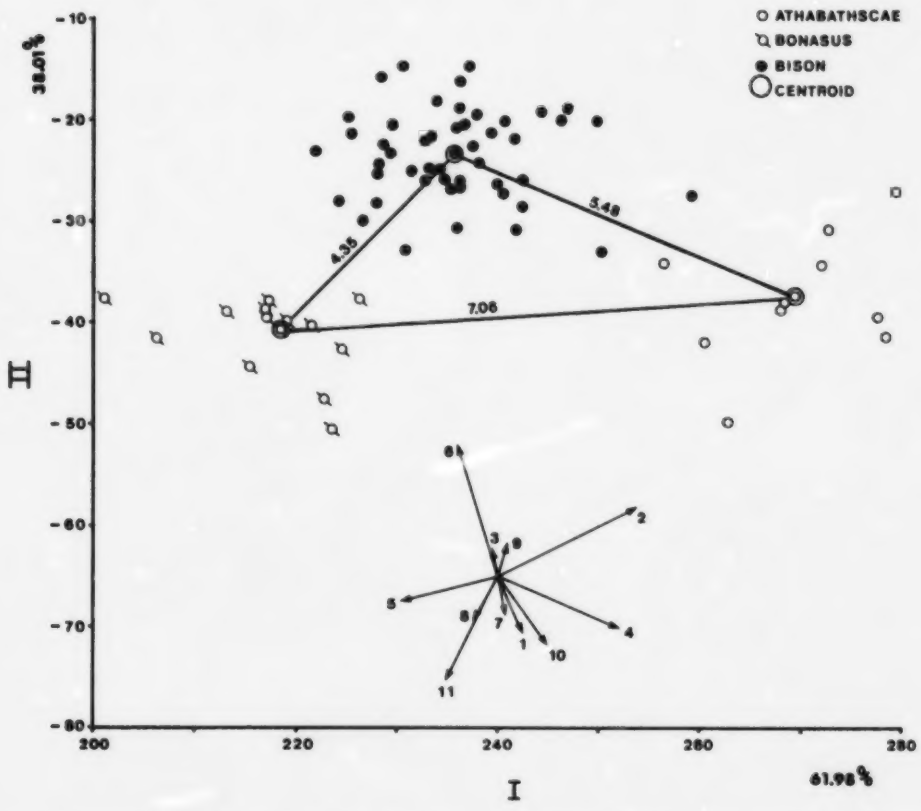


Figure 11. Projection of individual specimens and centroids of three taxa of modern bison onto the first two canonical variates, based on 11 cranial variables. Intercentroid distances (D) show the mutual relationship between taxa. Character vector lengths equal two standard deviations. 1 CHC; 2 GWA; 3 WHCO; 4 GPW; 5 AOW; 6 WMP; 7 RW2; 8 P2M3L; 9 M1M3L; 10 FP; 11 OC.

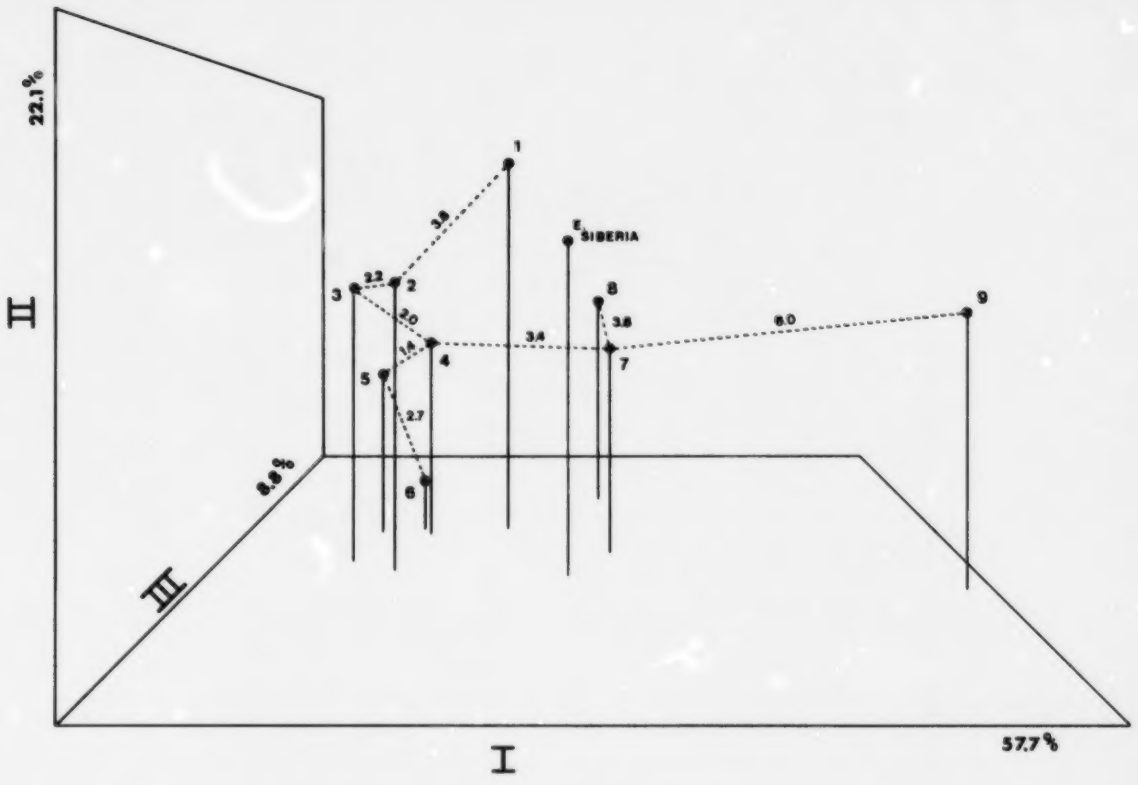


Figure 12. Three dimensional projection of the centroids of modern (1-6), early to mid-Holocene (7 and 8) and late Pleistocene bison (9) onto the first three canonical axes. The superimposed minimum spanning tree connects nearest neighbors. 1-*athabascae*; 2-CP; 3-CGP; 4-USRM; 5-SGP; 6-EUS; 7-*occidentalis*; 8-*antiquus*. 9-*priscus*, The east Siberian bison (see text) was scored as an unknown to determine its affinities to the North American taxa.

pared to those of subfossil Holocene bison from Alberta (Duffield, Fort Saskatchewan, Spirit River) using seven variables (Figure 14). The results, nearly identical to those in Figure 9, are interesting in that they show subfossil bison to be highly similar to modern *athabascae* with respect to the dimensions compared.

Although none of the specimens used had been radiocarbon dated, other specimens from Duffield and Fort Saskatchewan that have been dated (McDonald 1981, Harington pers. comm.) suggest ages of between 4000 and 8000 BP for these sites.

Harington (1984) described a cranial fragment from Banff, referred by him to *B. b. occidentalis*, which yielded a radiocarbon date of 3240 ± 90 yrs BP. This demonstrates that *occidentalis-athabascae*-like bison lingered in western Alberta, an area occupied by *B. b. bison* in historic times, until relatively recently.

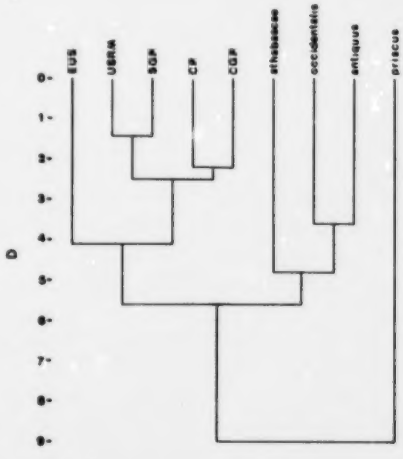


Figure 13. Dendrogram summarizing the distance relationships between modern (EUS, USRM, SGP, CP, CGP, *athabascae*), early to mid Holocene (*occidentalis*, *antiquus*), and late Pleistocene bison (*priscus*) in four-dimensional canonical variate space. The cophenetic correlation coefficient is 0.89.

Table 1. Means and Standard deviations for 11 cranial variables in historical, Holocene and late Pleistocene bison

Measurement	*B. b. athabascae* (N = 12)		CP (N = 10)		CGP (N = 33)		USRM (N = 12)		SGP (N = 15)		EUS (N = 2)		PR (N = 6)		*occidentalis* (N = 31)		*antiquus* (N = 4)		*priscus* (N = 3)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1. Length, occipital crest to nasofrontal suture (ON)	260.3	13.03	238.8	11.19	242.6	12.78	250.0	15.70	246.9	9.58	259.5	6.36	251.4	11.69	257.4	12.34	277.2	15.11	274.0	6.24
2. Vertical diameter of horn core (VD)	94.1	7.24	78.1	4.82	81.6	7.49	85.4	6.44	83.1	5.26	80.0	9.90	95.5	12.72	93.9	7.20	108.0	4.08	102.7	12.01
3. Transverse diameter of horn core (TD)	98.7	9.50	82.7	4.00	80.1	6.74	87.0	8.28	83.5	3.91	78.5	4.95	95.5	10.36	97.3	8.65	108.0	4.76	118.3	12.22
4. Greatest auditory width (GWA)	286.6	10.08	257.7	11.70	261.1	10.74	254.5	8.99	242.4	8.89	227.5	0.71	264.3	10.36	260.0	12.08	283.5	10.28	273.0	5.20
5. Width of condyles (CW)	127.4	8.47	123.8	5.25	125.9	6.04	129.9	6.60	125.0	5.58	126.5	3.54	136.9	7.48	132.5	6.04	147.0	5.89	140.0	1.00
6. Width of cranium between horn cores and orbits (WHCO)	295.7	8.60	265.1	15.47	267.0	10.65	273.8	12.34	267.8	7.97	274.5	12.02	278.5	19.37	292.1	12.51	312.0	22.69	297.7	25.15
7. Greatest Postorbital width (GPW)	357.9	11.66	328.7	7.56	319.6	13.79	329.8	15.89	324.1	12.58	316.5	6.36	342.9	15.51	344.2	14.59	369.0	30.12	348.7	18.77
8. Spread of horn cores tip-to-tip (SHTT)	700.8	64.41	597.8	39.56	587.2	55.01	623.0	36.36	586.4	34.91	605.0	57.98	670.0	66.93	758.1	71.29	832.2	37.51	944.0	92.26
9. Length of core on upper curve tip-to-burr (CLUC)	242.8	35.19	190.1	19.94	189.2	27.39	198.7	20.32	177.5	21.27	185.0	16.97	234.0	19.49	275.4	34.37	267.0	14.63	400.3	14.15
10. Length, tip of core to upper burr (TB)	213.2	25.67	175.5	17.76	169.4	23.10	180.7	16.28	162.6	15.94	162.0	22.63	212.6	18.95	242.1	25.44	241.2	15.44	345.3	12.90
11. Circumference of horn-core (CHC)	288.0	18.00	252.0	18.57	253.1	20.07	266.8	24.20	255.3	13.49	243.0	22.63	305.5	34.88	295.5	24.91	325.8	10.14	336.3	24.54

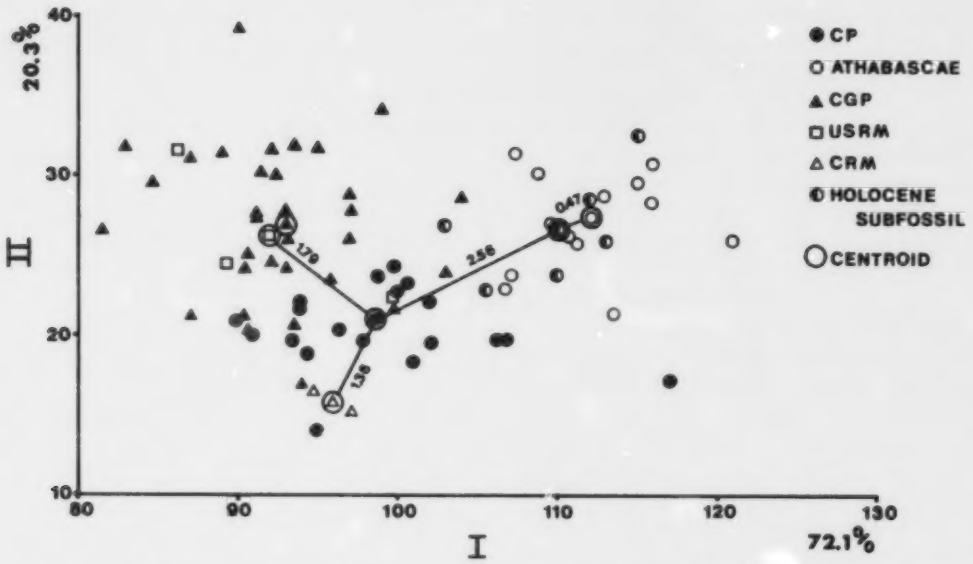


Figure 14. Projection of individual specimens and centroids of geographic subsamples of *B. bison* and subfossil Holocene bison from Alberta onto the first two canonical variates, based on seven cranial characters, and showing minimum spanning tree with distances (D).

To examine further the morphometric relationship of the modern forms of bison to earlier Holocene and late Pleistocene forms including those from Eurasia, a PCA on a correlation matrix of 8 cranial variables was done after standardizing the data (Figure 15). The similar values and positive signs of the character loadings on the first PC axis show variation in size to be mainly along this axis. The second axis separates the forms on the basis of shape i.e. relative horn dimensions (SHTT, CLUC, TB) and cranial width measurements (GWA, WHCO and GPW). The Holocene and late Pleistocene representatives are situated to the right, while the smaller modern forms are predominantly on the left (*athabascae* is the notable exception). The forms with relatively wider skull dimensions and relatively shorter horns are found high along the second axis, those with longer horns and relatively narrower skulls lower down. The MST linking nearest neighbors, based on the distance matrix and projected onto the first two principal components, shows the craniometric relationships between the forms compared (Figure 15).

The interesting points that emerge from this analysis are the divergent position of *B. b. athabascae* among modern bison; its great similarity to Holocene forms and the general similarity of Holocene and late Pleistocene bison of Eurasia and North America.

The morphometric variation among modern, Holocene and late Pleistocene bison expressed in the above analyses provides a guide for the interpretation of the taxonomic relationships among them. The graphs in Figure 12 and 15 suggest that the variation within modern bison may be similar to that found among Holocene and late Pleistocene forms as well as that between modern and Holocene forms. For example the greatest distance (D = 7.68) between modern forms of bison in Figure 12, that between *B. b. athabascae* and EUS, exceeds that between *occidentalis* and *antiquus* (D = 3.63) and that between *occidentalis* and *priscus* (D = 6.00); and is only slightly less than that between *antiquus* and *priscus* (D = 7.80). In other words, variation within modern and late Pleistocene-Holocene bison is quite similar. If we now examine the differences between modern bison and late Pleistocene-Holocene bison (D 3.38–6.00), we find them to be of a similar magnitude to those found among modern bison (D 1.41–7.68). Similarly in Figure 15 the greatest distance (calculated following Goodman 1972) between modern forms is that between *athabascae* and *bonasus* (D = 3.33), again exceeding that between *occidentalis* and *antiquus* (D = 1.56) as well as that between *priscus* and these two (D = 2.37 and 3.19 respectively). The distances between geographic samples of modern bison range from 0.15 (CGP-CP) to 3.33 (*athabascae*-

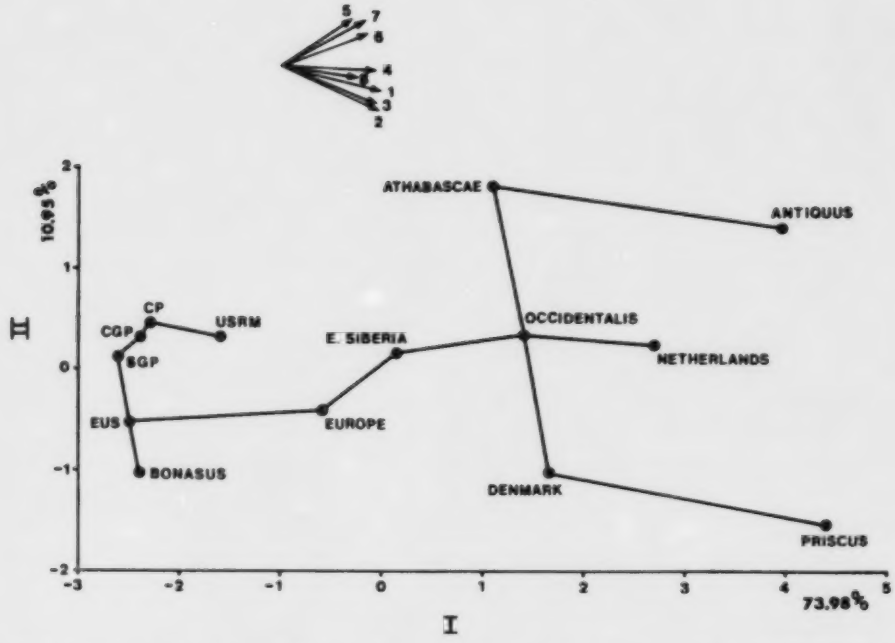


Figure 15. Relationships among modern, Holocene and late Pleistocene bison from North America and Eurasia, on the basis of the first two principal components using eight cranial variables. The dots represent centroids of samples or individual specimens (Holocene or late Pleistocene specimen from eastern Siberia, Denmark, and the Netherlands) which are joined by a minimum spanning tree. Character vectors show the relationship of the eight original variables and the principal components. The first axis represents size variation, the second axis shape. 1 SHTT; 2 CLUC; 3 TB; 4 CHC; 5 GWA; 6 WHCO; 7 GPW; 8 ON. Data for Denmark and Europe centroid from Degerbøl and Iversen (1945).

bonasus), those between modern and Holocene bison from 0.78 (EUS-subfossil European) to 3.71 (*bonasus-antiquus*). Thus the degree of difference within the living subspecies is similar to that within late Pleistocene-Holocene bison as well as to that between modern and Holocene bison.

If we take the amount of morphological difference between the most divergent modern subspecies to indicate how much morphological difference may evolve without the acquisition of reproductive isolation (Mayr 1969), we are led to the conclusion that modern and late Pleistocene-Holocene bison are only subspecifically distinct.

The proximity of the eastern Siberian specimen to *occidentalis* and *athabascae* in Figures 12 and 15 is of particular interest, because of the significance of this specimen in interpreting the recent evolutionary history of North American bison. Univariate comparisons of 18 measurements of this specimen with those of the *occidentalis* and *athabascae* samples, using a *t* test (Simpson et al. 1960) showed none of the differences with *occidentalis* to be significant. Only two measurements differed significantly from those of *athabascae* (WHCO, $t = 3.5335$ $P < .01$ and WMP $t = 2.0192$ $P < .05$).

The similarity between *occidentalis* and *athabascae* is further evident from the ratio diagram (Figure 16) comparing 19 cranial dimensions in *B. b. bison*, *B. b. athabascae* and *B. b. occidentalis*. *B. b. bison* shows greater deviations from *B. b. occidentalis* than *B. b. athabascae* does. The differences are most marked in the horn measurements (SHTT, CLUC, TB, VD, TD, CHC) reflecting the general reduction in the size of the horns in *B. b. bison*. Of the other cranial dimensions the most obvious differences are exhibited in OC which is smaller in *B. b. bison* and in the tooth row measurements P2M3L, M1M3L which are relatively larger in *B. b. bison*.

In *B. b. athabascae* the main difference from *B. b. occidentalis* is in the reduced horn length measurements (SHTT, CLUC, TB). Deviations from the *occidentalis* pattern are considerably less than in *B. b. bison*. The thickness of the horn core in *B. b. athabascae* (VD, TD, CHC) has changed relatively little compared to that of *B. b. occidentalis*, in contrast to the situation in *B. b*

bison. The remaining cranial variables in *B. b. athabascae* are generally similar to those in *occidentalis*.

4. Morphometric Analyses of Present Remnant Populations in Canada

a) Craniometric comparisons of adult males. The taxonomic affinities of present Canadian plains bison herds (AP) relative to the historical bison populations were determined by scoring AP as an unknown in two CVA's of historical populations using the sample means of AP for 11 variables (Figures 17 and 18). In both cases the AP mean values produced canonical variate scores close to the centroids of historical northern plains populations. Present Canadian populations of plains bison (AP) are therefore craniometrically representative of historical northern plains bison and close to the original population once found on the Canadian prairies.

A CVA of adult AP and *athabascae* male reference samples, the two "parental" populations of the present bison populations in Wood Buffalo National Park, was used to determine the taxonomic affinities of the NR and SE specimens by scoring them as "unknowns" and plotting their positions on the AP-*athabascae* axis (Figure 19, Table 2). In addition a three-group CVA was done including NR as an *a priori* group (Figure 20). In Figure 19 both NR and SE specimens occupy a somewhat intermediate position on the AP-*athabascae* axis. The NR centroid is closer to that of *athabascae* than to that of AP. Of the 16 adult NR males, 10 (62.5%) fall within two standard deviations of the *athabascae* centroid, only three (18.75%) fall within two standard deviations of the AP centroid and three (18.75%) fall in between the two standard deviation limits of the reference samples. In other words 81.25% of the NR specimens fall outside the two standard deviations of the AP centroid.

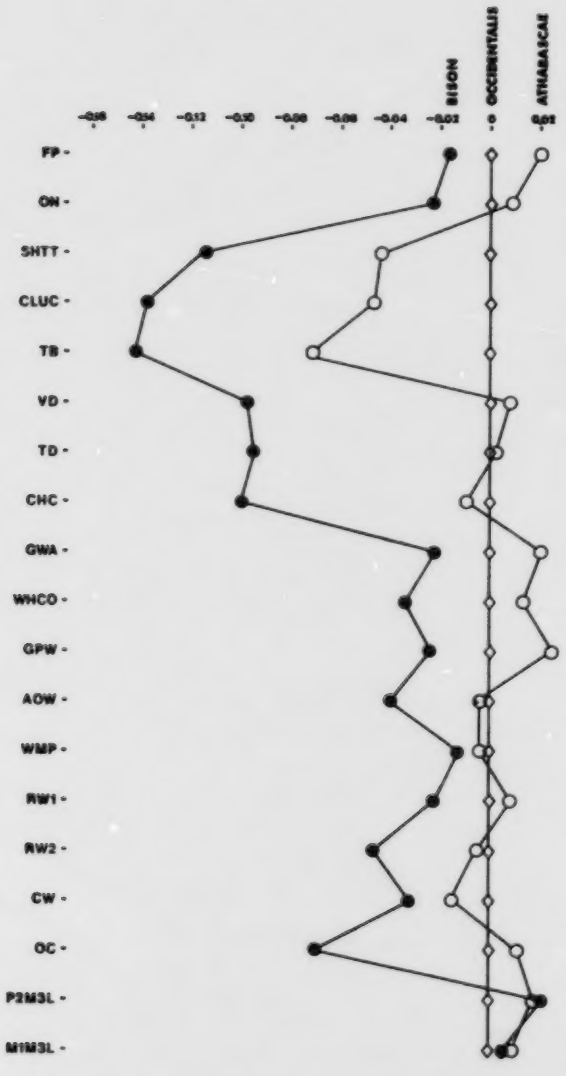


Figure 16. Ratio diagram comparing 19 skull dimensions in *B. b. bison*, *B. b. athabascae* and *B. b. occidentalis*, with the latter serving as a standard.

Table 2 Canonical variate coefficients for 11 cranial characters of adult male *B. b. athabascae* and AP bison (*B. b. bison*)

Character	Canonical variate coefficient
1. ON	-0.0658
2. VD	0.5633
3. TD	0.0730
4. GWA	0.2993
5. CW	-0.3765
6. WHCO	-0.0398
7. GPW	0.1706
8. P2M3L	0.0583
9. M1M3L	0.4204
10. OC	0.3536
11. WMP	-0.3254

The scores for the five SE specimens present a similar picture. Two (40%) fall within two standard deviations from the AP centroid, three (60%)

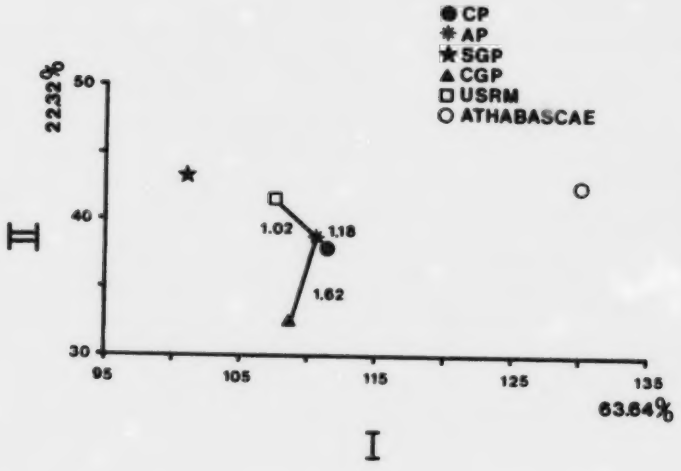


Figure 17. The morphometric relationship of present Canadian plains bison (AP) to historical populations of bison based on six horn and five cranial variables. Distances to nearest centroids are shown.

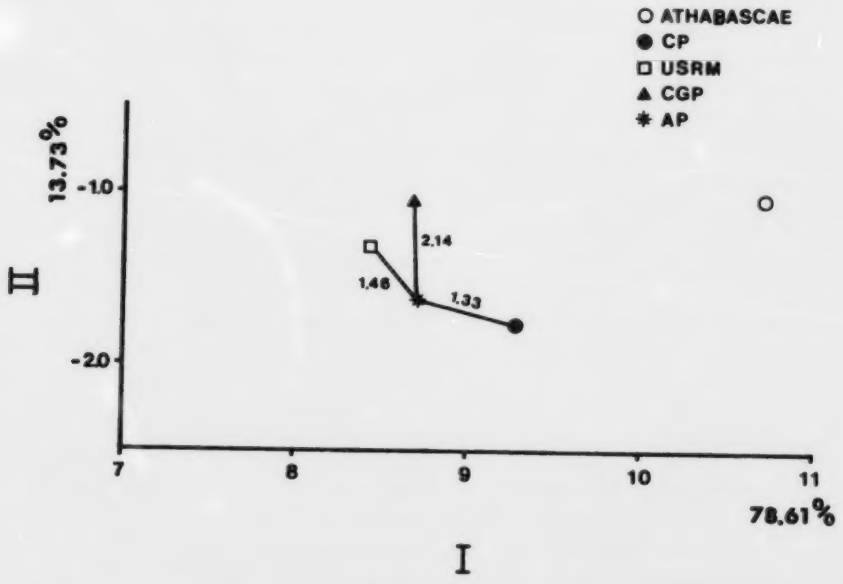


Figure 18. The morphometric relationship of present Canadian plains bison (AP) to historical populations of northern bison, based on nine cranial measurements and two horn measurements. Distances to nearest centroids are shown.

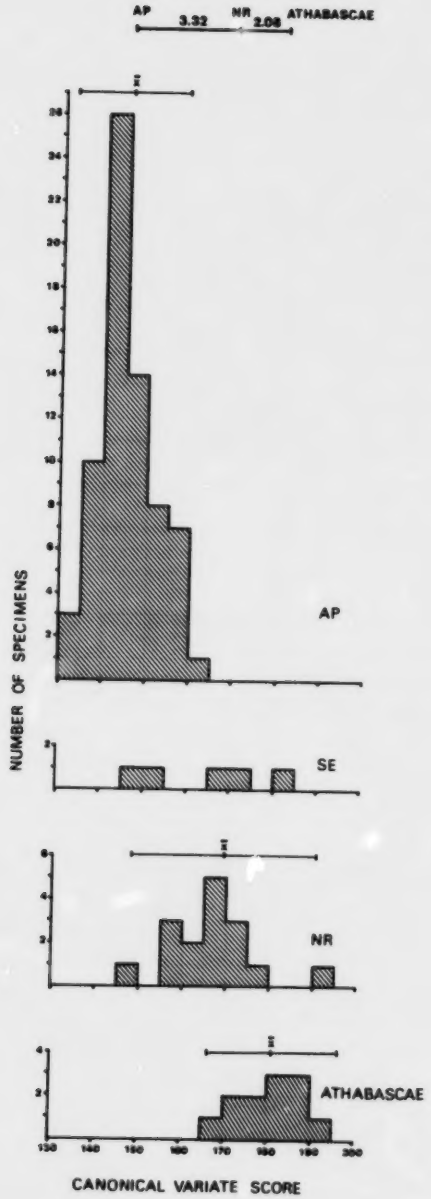


Figure 19. Histograms of canonical variate scores for four samples of adult male bison based on 11 cranial characters (see Table 2). AP and *athabascae* serve as reference samples. SE and NR were scored as unknowns on the AP-*athabascae* axis. The mean score for each sample with two standard deviations on either side is shown directly above the histograms. The distances of the NR centroid to the centroids of the reference samples is shown at the top of the graph.

fall within the two standard deviations range of the *athabascae* centroid.

Three-group CVA produced quite similar results (Figure 20), with the NR sample being somewhat intermediate to AP and *athabascae*, but considerably closer to the latter.

A number of cranial dimensions of adult *athabascae*, NR and AP males (Table 3) were also compared using a ratio diagram (Simpson et al. 1960) with AP serving as a standard (Figure 21). The deviations of *athabascae* and NR from AP are on the whole remarkably similar with NR points paralleling those of *athabascae*, thus indicating that NR and *athabascae* skulls have nearly identical proportions and differ from AP skulls in similar ways. The position of most NR and *athabascae* points to the right of those of AP indicate larger size with *athabascae* generally being larger than NR. Differences in proportion lie in greater horn dimensions (SHTT, CLUC, TB, VD, TD and CHC showing the greatest deviations from AP) and relatively smaller WMP, CW, P2M3L, M1M3L and relatively larger OC. NR and *athabascae* differ significantly from AP in all measurements compared, except P2M3L and M1M3L (see Table 3).

The single measurements that best discriminate between *athabascae* and AP skulls are FP, WHCO and VD with probabilities of misidentification of 0.04 or less (Lubischew 1962) and corresponding percentages of joint nonoverlap of 96% or more. The best single discriminators between NR and AP are VD, CHC and FP with probabilities of misidentification of approximately 0.05, 0.06 and 0.11 and correspondingly lower percentages of joint nonoverlap than was the case in *athabascae* and AP.

NR and *athabascae* differed significantly in 6 out of the nineteen variables compared (OC, WHCO, GPW, FP, SHTT and CW) (Table 3). Of these OC, WHCO and GPW show the highest percentage joint nonoverlap (72, 70 and 69% respectively). The proportion of the above variables in NR, although more like *athabascae* show a tendency toward the condition in AP. For example OC is relatively larger in NR than one would expect if they had been drawn from the same population as *athabascae*. The variation of the characters in the three samples is highly similar judging from the coefficients of variability in Table 3. None of the observed differences were significant.

Table 3 Means, standard deviations, coefficients of variation and observed ranges of 19 cranial variables in adult bulls of *B. b. athabascae* NR and AP bison.

	athabascae					NR					AP					*t*-test	
	N	$\bar{x}$	SD	CV	Range	N	$\bar{x}$	SD	CV	Range	N	$\bar{x}$	SD	CV	Range	athabascae-NR	NR-AP
Basilar length (FP)	12	531.3	13.84	2.60	512–555	18	518.3	15.96	3.08	487–543	77	486.6	12.24	2.52	450–520	2.3005[a]	9.3141[c]
Length, occipital crest to nasofrontal suture (ON)	13	261.3	12.96	4.96	241–282	19	252.5	11.56	4.58	228–270	81	242.8	11.46	4.72	210–269	2.0139	3.3151[b]
Spread of horns, tip-to-tip (SHTT)	12	700.8	64.41	9.19	618–855	18	652.6	53.05	8.13	543–717	75	594.5	46.69	7.85	486–695	2.2383[a]	4.6172[c]
Core length on upper curve, tip-to-burr (CLUC)	13	242.2	33.74	13.93	195–323	18	226.9	26.15	11.52	160–262	80	196.4	19.54	9.95	152–250	1.4235	5.6037[c]
Length, tip of core to upper base at burr (TB)	13	212.8	24.62	11.57	187–270	18	205.6	21.8	10.61	158–233	80	176.2	17.72	10.06	139–220	0.8597	6.0890[c]
Vertical diameter of core (VD)	13	94.0	8.17	8.69	79–109	18	94.0	8.68	9.23	78–114	81	73.6	5.42	7.36	63–87	0.0194	12.7958[c]
Transverse diameter of horn core (TD)	13	97.4	10.20	10.47	82–118	18	94.2	11.63	12.34	72–118	83	78.2	6.34	8.12	68–94	0.7948	8.1853[c]
Circumference of horn core (CHC)	13	286.4	18.28	6.38	226–310	18	295.4	32.46	10.99	243–363	81	232.7	16.51	7.11	204–278	0.8993	11.8909[c]
Greatest width at auditory openings (GWA)	15	281.3	15.81	5.62	246–301	19	276.2	11.23	4.07	256–295	78	255.9	8.78	3.43	229–276	1.0996	8.5375[c]
Width of cranium between horn cores and orbits (WHCO)	13	295.4	8.29	2.81	283–313	19	285.4	9.63	3.37	269–301	82	265.0	8.82	3.33	246–289	3.0471[b]	8.9295[c]
Greatest postorbital width (GPW)	13	358.0	11.08	3.10	341–385	19	346.9	10.81	3.12	324–364	81	318.1	12.23	3.84	282–352	2.8243[b]	9.4295[c]
Anterior orbital width at notch (AOW)	13	261.8	13.44	5.13	239–286	19	259.6	13.57	5.23	238–291	82	240.6	13.57	5.64	214–274	0.4521	5.4991[c]
Width of skull at masseteric processes (WMP)	13	196.8	7.54	3.83	180–210	19	197.6	8.17	4.14	184–212	83	189.8	9.10	4.79	160–206	0.2804	3.4307[c]
Rostral width at maxillary-premaxillary suture (RW1)	12	127.3	7.45	5.85	116–139	19	126.1	8.93	7.08	109–144	83	118.9	6.16	5.18	103–132	0.3874	4.1984[c]
Rostral width (RW2)	11	112.2	4.75	4.23	105–118	19	110.6	5.55	5.01	99–122	83	101.7	4.65	4.57	86–118	0.8001	7.2537[c]
Width of condyles (CW)	15	128.4	8.01	6.24	118–143	18	133.3	5.54	4.16	120–145	77	123.4	5.19	4.21	116–138	2.0708[a]	7.1948[c]
Width of occipital constriction (OC)	14	183.4	14.36	7.83	162–205	19	168.0	12.69	7.56	146–189	69	152.2	11.54	7.58	125–174	3.2590[b]	5.1725[c]
P2M3 length (P2M3L)	13	149.2	6.82	4.57	143–161	19	146.9	8.52	5.80	129–160	83	150.3	5.31	3.53	131–162	0.8104	2.2223[a]
M1M3 length (M1M3L)	13	94.6	4.03	4.26	88–103	19	93.0	3.64	3.92	87–102	83	94.0	3.90	4.14	80–103	1.1695	1.0201

[a] $P < .05$
[b] $P < .01$
[c] $P < .001$

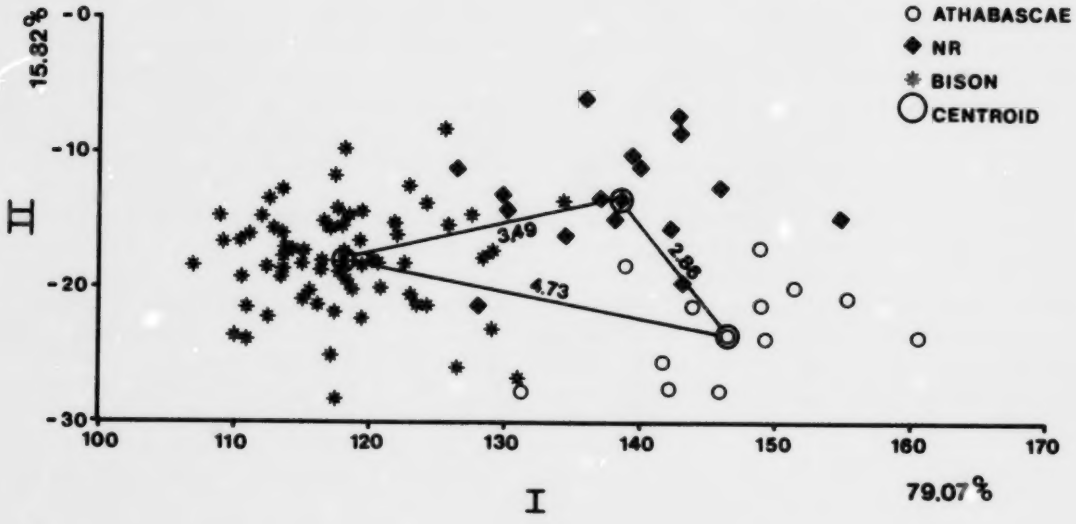


Figure 20. Projection of individual specimens and centroids of AP, NR and *athabascae* males onto the first two canonical variates based on 11 cranial variates showing intercentroid distances (D).

b) Craniometric comparisons of adult females. Analyses of the adult female samples produced results similar to those obtained for the males. The two-group CVA of AP and NR specimens shows a similar degree of overlap to that found in the males (Figure 22, Table 4). The generalized distance between NR and AP centroids is somewhat less than that in the males. Of the 10 NR female specimens 2 (20%) fall within two standard deviations from the AP centroid, or 8 (80%) lie outside the two standard deviations limits. The score for the *athabascae* female (NMC 10405) falls within one standard deviation to the left of the NR centroid and just outside the two standard deviation limit of the AP centroid. If the distance relationships of AP and *athabascae* cows were similar to that observed in the males, the position of NMC 10405 would be toward the lower limit of the *athabascae* distribution. The position of two SE and two WBNP females is similar to that of the SE males.

The three group CVA produced similar results (Figure 23) and underlines the existence of a morphometric relationship between NR and AP females which is essentially the same as that found between the males of these groups. The position of the single *athabascae* female relative to the AP and NR centroids is similar to that of the *athabascae* males in Figure 20.

The ratio-diagram comparing 19 dimensions of AP and NR adult female crania as well as those of NMC 10405 (Table 5), shows deviations in NR and *athabascae* from the standard (AP) similar to those in the male crania (Figure 24), but to a lesser extent. NR females differed from AP females significantly in 13 out of the 19 measurements compared in the ratio-diagram (Table 5). The best univariate discriminators between NR and AP females were GPW, WHCO, RW, and GWA, but

Table 4 Canonical variate coefficients for 11 cranial characters of adult female AP (*B. b. bison*) and NR bison

Character	Canonical variate coefficient
1. ON	-0.0904
2. VD	0.4559
3. TD	-0.3054
4. GWA	0.0482
5. CW	0.0063
6. WHCO	0.2168
7. GPW	0.0068
8. P2M3L	-0.5779
9. M1M3L	0.4983
10. OC	0.1089
11. WMP	-0.2174

the probabilities of misidentification were considerably higher than those found in the equivalent male samples (P≈0.16, 0.18, 0.19 and 0.21 respectively). Variation of the characters in AP and NR samples is quite similar (see coefficients of variation in Table 5).

The single *athabascae* specimen closely parallels the NR sample, suggesting that NR female crania closely resemble those of the original *B. b. athabascae*. Comparison of the cranial measurements with the means for the NR sample showed that there were no significant differences (Table 5). On the other hand comparison with the AP sample demonstrated significant differences in five variates (GWA, WHCO, GPW, AOW, WMP, see Table 5).

c) Morphometric comparison of mandibles.
CVA of 15 mandibular measurements of *athabascae*, AP and NR bulls yielded results similar to those for the cranial variables. The NR specimens are intermediate to AP and *athabascae*, but closer to the latter (Figure 25). Basic statistics for adult bulls and cows are listed in Tables 6 and 7.

d) Sexual dimorphism of the cranium in AP and NR bison.
Sexual dimorphism of the skulls of NR and AP specimens was analyzed by CVA of 11 cranial variables. The degree of sexual dimorphism in the skulls of both groups was almost identical (Table 8). In both there is complete separation between male and female skulls, and the distance between the centroids of males and females is highly similar. The relative contribution to the dis-

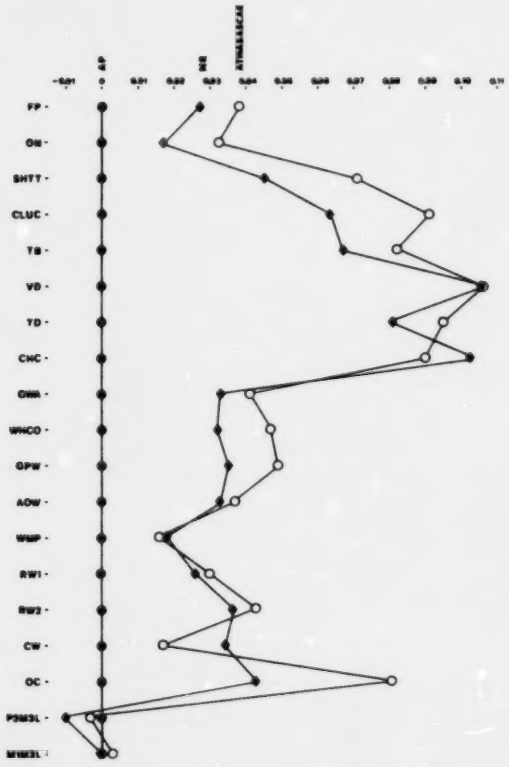


Figure 21. Ratio diagram comparing 19 skull dimensions (see Table 3) in adult male *athabascae*, NR and AP with the latter serving as a standard.

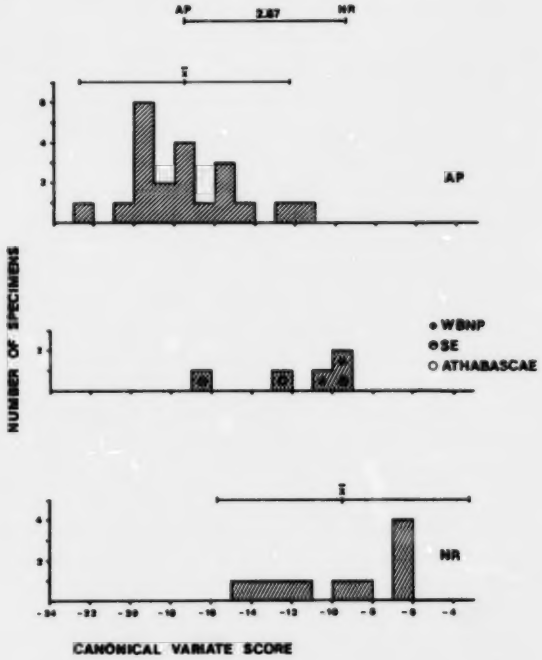


Figure 22. Histograms of canonical variate scores of three samples of adult female AP and NR bison based on 11 cranial variables. WBNP and SE specimens as well as the single *athabascae* specimen were scored as unknowns on the AP-NR axis. The mean scores for AP and NR samples, with two standard deviations on either side of the centroid is shown directly above the histograms. The distance (D) between AP and NR centroids is shown at the top of the graph.

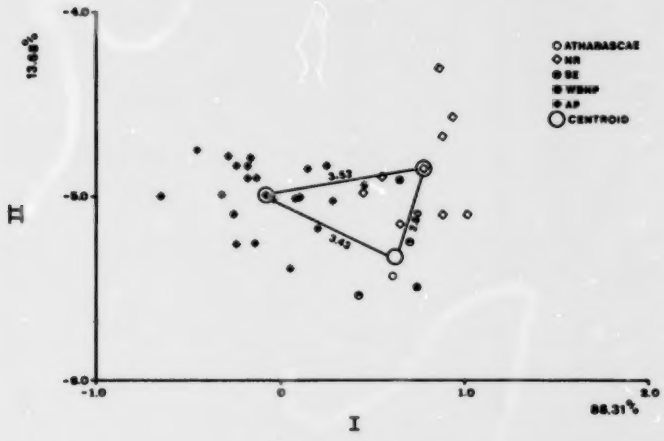


Figure 23. Projection of individual specimens and centroids of AP, NR, *athabascae*, SE and WBNP females onto the first two canonical variates with intercentroid distances. The CVA was based on 11 cranial variables. SE, WBNP and the single *athabascae* specimen were combined as one *a priori* group, whose centroid is represented by the empty circle.

Table 5 Means, standard deviations, coefficients of variation and observed ranges of 19 cranial variables in adult cows of NR and AP bison, with measurements of a single *B. b. athabascae* cow.

Measurement	*athabascae*	NR					AP					*t*-test
	(N=1)	N	$\bar{x}$	SD	CV	Range	N	$\bar{x}$	SD	CV	Range	NR-AP
Basilar length (FP)	467	11	460.7	13.22	2.87	441–485	25	443	11.79	2.66	415–468	4.0006[c]
Length, occipital crest to nasal-frontal suture (ON)	217	15	208.6	9.68	4.72	188–226	33	209	8.66	4.14	184–225	n.s.
Spread of horns, tip-to-tip (SHTT)	435	14	459.1	37.61	8.19	401–515	25	438	40.89	9.33	359–517	2.6379[a]
Core length on upper curve, tip-to-burr (CLUC)	147	15	146.2	27.84	19.03	103–182	34	123	23.22	18.90	63–162	3.0410[b]
Length, tip of core to upper base at burr (TB)	134	15	132.2	20.37	15.41	98–159	34	115	19.69	17.19	63–145	2.7891[b]
Vertical diameter of core (VD)	51	16	50.1	5.98	11.93	43–64	35	44	4.98	11.30	30–52	3.8094[c]
Transverse diameter of horn core (TD)	54	16	51.9	6.27	12.07	41–62	35	48	4.97	10.37	32–56	2.3926[a]
Circumference of horn core (CHC)	164	16	163.1	18.06	11.07	139–199	34	148	22.76	15.35	100–248	2.3317[a]
Greatest width at auditory openings (GWA)	220	14	218.3	9.87	4.52	205–240	24	205	6.98	3.40	189–220	4.8787[c]
Width of cranium between horn cores and orbits (WHCO)	227	16	224.6	9.20	4.09	210–242	34	209	8.10	3.88	190–222	6.1180[c]
Greatest postorbital width (GPW)	284	16	280.8	14.92	5.09	262–309	35	257	10.13	3.94	237–275	6.8287[c]
Anterior orbital width at notch (AOW)	214	16	208.5	13.55	6.50	195–245	35	191	9.45	4.94	174–211	5.3527[c]
Width of skull at masseteric processes (WMP)	177	16	170.4	8.50	4.99	155–186	36	164	6.82	4.16	153–179	2.9285[b]
Rostral width at maxillary-premaxillary suture (RW1)	114	14	101.5	6.91	6.80	89–112	36	99	5.64	5.67	83–110	n.s.
Rostral width (RW2)	92	11	92.6	4.89	5.28	86–102	36	85	4.10	4.81	76–93	5.2054[c]
Width of condyles (CW)	118	13	113.8	6.53	5.73	102–127	21	113	4.23	3.76	102–120	n.s.
Width of occipital constriction (OC)	128	15	126.1	9.77	7.74	112–148	32	118	11.42	9.67	97–136	2.1695[a]
P2M3 length (P2M3L)	141	16	138.9	11.34	8.14	123–154	36	147	4.49	3.06	137–158	3.7047[c]
M1M3 length (M1M3L	89	16	92.2	5.49	5.95	86–109	36	92	3.36	3.64	84–99	n.s.

[a] $P < .05$
[b] $P < .01$
[c] $P < .001$

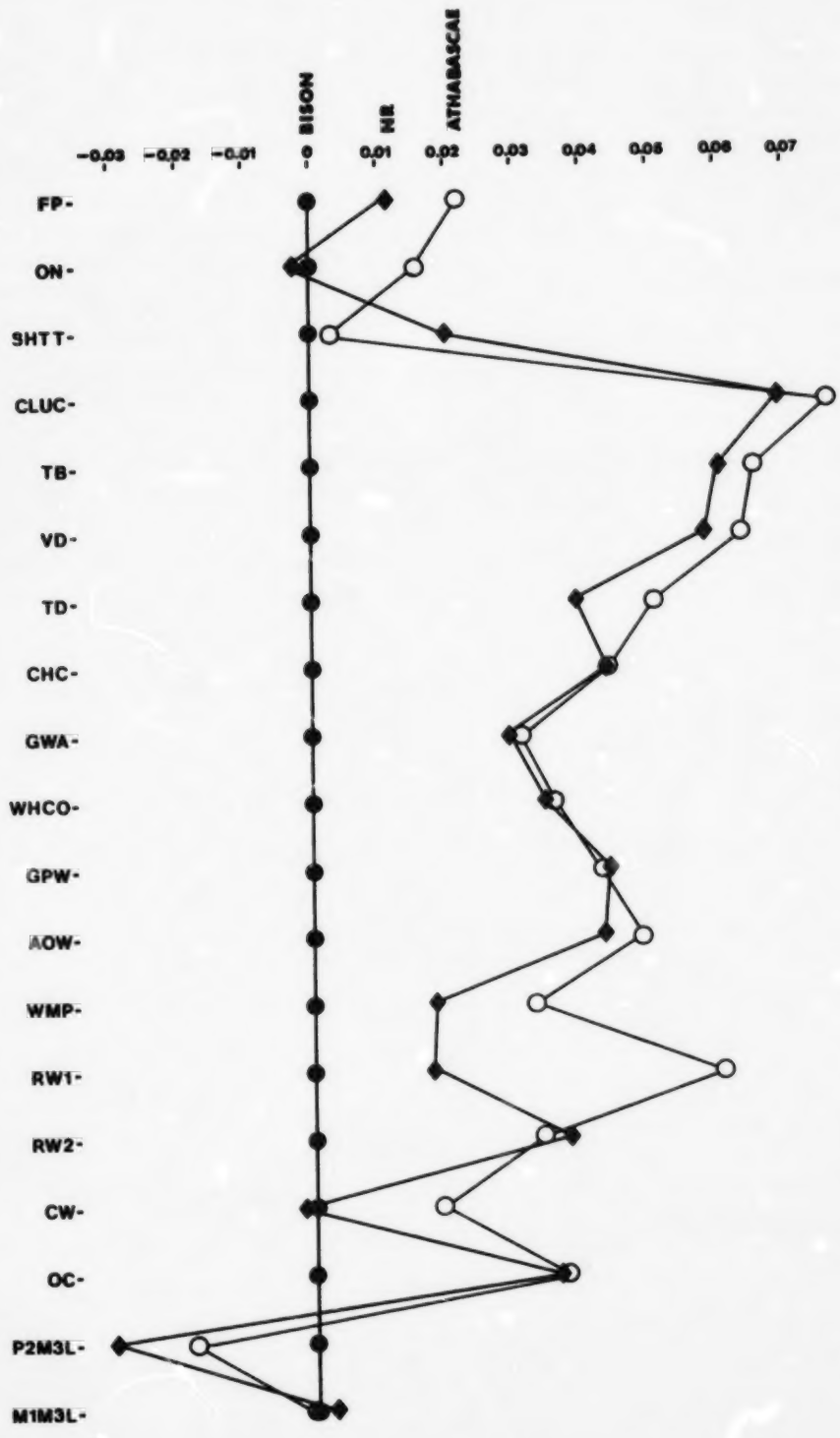


Figure 24. Ratiodiagram comparing 19 skull dimensions (see Table 5) in adult female *athabascae*, NR and AP bison, with the latter serving as a standard.

Table 6 Means, standard deviations, coefficients of variation and observed ranges of 15 mandibular variables in adult bulls of *B. b. athabascae*, NR and AP bison.

	athabascae (N = 8)				NR (N = 17)				AP (N = 75)				*t*-test *athabascae*-	
	$\bar{x}$	SD	CV	Range	$\bar{x}$	SD	CV	Range	$\bar{x}$	SD	CV	Range	NR	NR-AP
6 Length pm2-m3 (pm2 m3L)	161.7	11.27	6.96	152–186	156.5	4.51	2.88	151–164	159.0	5.45	3.42	144–170	n.s.	n.s.
7 m1-m3 alveolar length (m1m3L)	103.5	4.24	4.09	98–110	101.4	3.08	3.03	97–107	103.1	4.03	3.90	92–112	n.s.	n.s.
9 Height of coronoid proc. (HCP)	57.2	9.94	17.37	34–66	60.7	3.47	5.71	52–68	58.7	3.36	5.72	52–67	n.s.	2.1698[a]
10 Width of coronoid proc. (WCP)	50.3	6.95	13.81	35–59	50.8	2.57	5.05	46–59	48.0	3.31	6.89	40–59	n.s.	3.3132[b]
11 Width of articulating proc. (WAP)	89.2	3.58	4.01	83–93	85.5	4.54	5.30	78–96	82.6	3.86	4.67	76–92	n.s.	2.7061[b]
12 Posterior of m3 to mandibular foramen (PM3F)	93.2	8.58	9.20	78–103	83.0	6.13	7.38	73–93	74.9	5.18	6.91	62–87	3.4312[b]	5.6036[c]
13 Posterior of m3 to posterior edge of articulating proc. (Pm3AP)	206.0	7.33	3.55	193–216	195.6	7.33	3.74	186–212	174.0	6.42	3.68	160–199	3.2933[b]	12.1888[c]
14 Width of ramus at posterior of m1. (WR)	31.6	2.07	6.55	29–36	32.4	3.00	9.25	28–40	29.9	1.61	5.38	26–34	n.s.	4.8373[c]
16 Width of mandibular condyle (WMC)	57.0	2.39	4.19	52–60	55.2	2.59	4.69	50–59	50.9	2.94	5.77	43–57	n.s.	5.6469[c]
17 m2 alveolar to base height (MD)	61.8	2.17	3.51	59–65	64.5	3.36	5.20	59–70	62.8	2.98	4.74	56–70	2.0741[a]	2.0742[a]
18 Width of m3 (Wm3)	19.2	1.40	7.29	18–22	18.3	1.65	9.01	16–22	18.3	1.19	6.50	15–21	n.s.	n.s.
19 Width of m2 (Wm2)	20.8	1.22	5.86	19–23	18.9	1.93	10.21	16–22	19.0	1.22	6.42	16–22	2.5666[a]	n.s.
20 Width of m1 (Wm1)	19.0	0.63	3.31	18–20	18.7	0.91	4.86	17–20	17.6	0.86	4.88	16–20	n.s.	4.4976[c]
21 Length of pm2–m1 (pm2m1)	56.6	3.58	6.32	52–63	55.6	2.27	4.08	52–59	54.9	2.96	5.39	48–61	n.s.	n.s.
22 Substitute Total length (STL)	383.7	12.87	3.35	359–396	378.5	9.62	2.54	358–394	361.1	7.36	2.03	342–375	n.s.	8.2942[c]

[a] $P < .05$
[b] $P < .01$
[c] $P < .001$

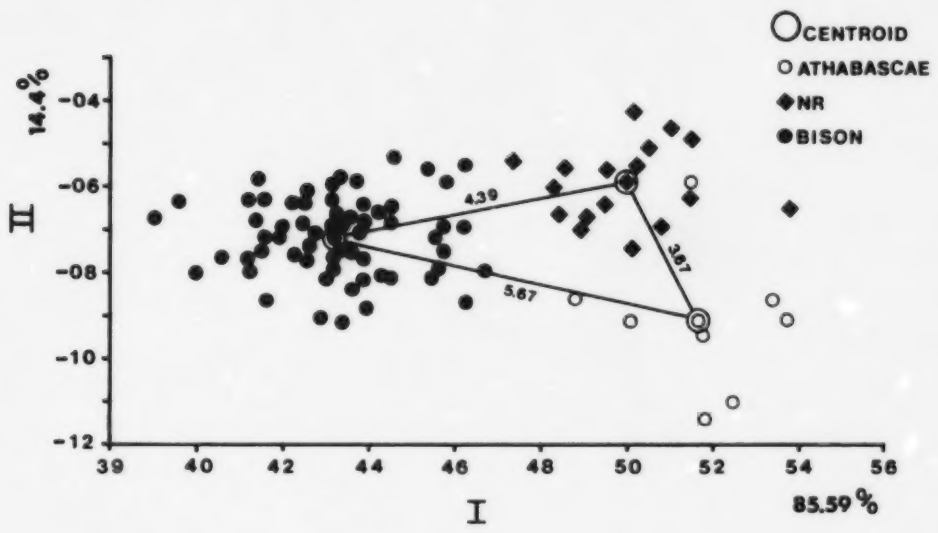


Figure 25. Projection of individual specimens and centroids of adult male AP, NR and *athabascae* onto the first two canonical variates with intercentroid distances (D). The analysis was based on 15 mandibular measurements.

Table 7 Means, standard deviations, coefficients of variation and observed ranges of 15 mandibular variables in adult cows of *B. b. athabascae*, NR and AP bison.

	athabascae	NR (N = 5)				AP (N = 37)				
	(N = 1)	$\bar{x}$	SD	CV	Range	$\bar{x}$	SD	CV	Range	*t*-test
6 Length pm2-m3 (pm2m3L)	151	156.6	6.27	4.00	151–166	155.2	4.77	3.07	145–167	n.s.
7 m1-m3 alveolar length (m1m3L)	95	102.7	3.77	3.67	98–107	101.2	3.34	3.30	94–108	n.s.
9 Height of coronoid proc. (HCP)	62	58.4	3.51	6.01	54–63	54.3	2.63	4.84	48–61	3.1510[b]
10 Width of coronoid proc. (WCP)	49	46.6	2.88	6.18	43–51	44.7	1.53	3.42	41–47	2.3271[a]
11 Width of articulating proc. (WAP)	77	78.6	4.72	6.00	72–83	74.0	3.01	4.06	69–81	2.9962[b]
12 Posterior of m3 to mandibular foramen (Pm3F)	77	74.6	10.36	13.88	59–84	60.5	5.39	8.90	44–70	4.8728[c]
13 Posterior of m3 to posterior edge of articulating proc. (Pm3AP)	172	174.8	16.12	9.22	151–192	149.2	6.19	4.14	130–162	6.9092[c]
14 Width of ramus at posterior of m1.(WR)	28	29.6	1.67	5.64	28–32	28.6	1.72	6.01	26–34	n.s.
16 Width of mandibular condyle (WMC)	48	49.2	4.38	8.90	43–55	47.0	2.08	4.42	42–50	n.s.
17 m2 alveolar to base height (MD)	57	60.4	2.30	3.80	58–64	59.8	3.26	5.45	54–68	n.s.
18 Width of m3 (Wm3)	18	17.6	1.67	9.48	16–20	17.4	1.28	7.35	15–20	n.s.
19 Width of m2 (Wm2)	18	18.0	2.00	11.11	16–21	18.0	1.30	7.22	15–20	n.s.
20 Width of m1 (Wm1)	17	17.8	0.84	4.71	17–19	17.0	0.95	5.58	15–19	n.s.
21 Length of pm2-m1 (PL)	53	54.6	2.70	4.94	52–59	52.9	2.44	4.61	49–58	n.s.
22 Substitute Total length (STL)	345	370.0	12.75	3.44	356–385	336.0	10.89	3.24	310–365	6.4342[c]

[a] $P < .05$
[b] $P < .01$
[c] $P < .001$

Table 8 Standardized discriminant coefficients for 11 cranial variables in adult AP and NR bison and the distance (D) between the centroids for males and females, illustrate the nature and degree of sexual dimorphism of the crania.

	AP	NR
ON	0.1378	-0.1642
VD	0.1796	0.4554
TD	-0.0321	-0.5335
GWA	0.4417	0.1703
CW	-0.0062	0.2100
WHCO	0.3786	0.3228
GPW	-0.1529	0.3713
P2M3L	0.1395	-0.0784
M1M3L	-0.1892	-0.1432
OC	0.0804	-0.3639
WMP	-0.0256	-0.0946
	D ♂♂-♀♀ = 8.3	D ♂♂-♀♀ = 8.3

crimination by individual variables differs somewhat between the two samples on the basis of the standardized canonical variate coefficients. Overall size and larger horn and cranial width dimensions in the males are the principal dimorphic chracteristics.

The five best univariate discriminators (with approximate probabilities of misidentification) in AP bison are: GWA ($P < .0003$); WHCO ($P < .0007$); VD ($P \approx .003$); GPW ($P < .005$); TD ($P \approx .006$). In NR they are the same variables but in a somewhat different order WHCO ($P < .003$); GWA ($P < .008$), VD ($P < .01$); GPW ($P \approx .01$) and TD ($P \approx .02$).

e) Morphometric comparisons of the postcranial skeleton.

The plot of the first two principal components from the analysis of 25 postcranial variables shows

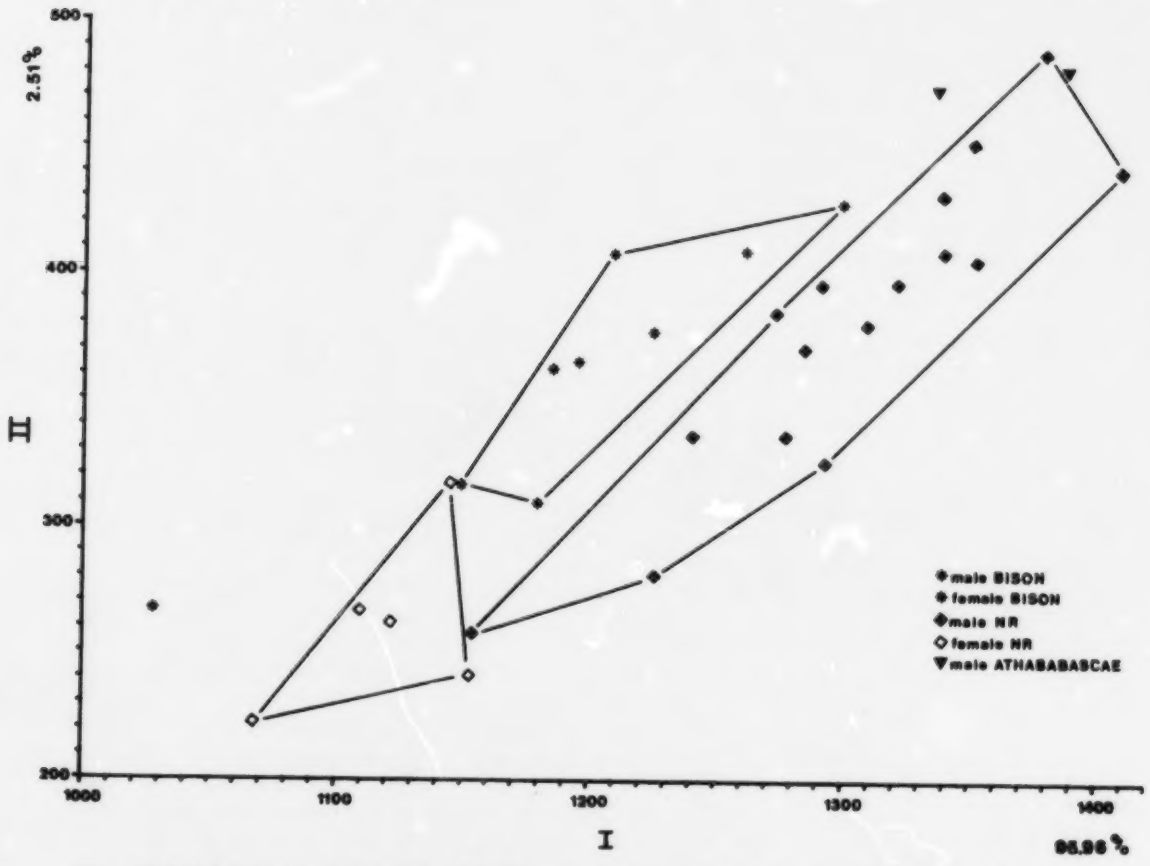


Figure 26. Relative position of specimens of *B. b. bison*, *B. b. athabascae* and NR in the projection on the first two principal components of a correlation matrix of 25 postcranial characters (see Table 8). Note the position of the single female *B. b. bison*.

a clear separation of plains bison on the one hand and *athabascae* and NR on the other into distinct clusters (Figure 26). The loadings on the first two components (Table 9) show those of the first component to be all of the same sign and nearly the same magnitude. We may, therefore, interpret the first component as predominantly a size component. The second principal component has loadings of varying sizes and mixed signs, and can be said to summarize shape (Jolicoeur and Mosimann 1960). The variation along the principal axes of the bivariate frequency ellipses represents size variation, with smaller individuals situated towards the lower left corner of the graph and the larger ones toward the upper right corner. Deviations at right angles of the principal axes represent largely variation in shape. The different elevations of the plains bison and NR cluster relative to each other indicate differences in proportions of some of the postcranial elements. Examination of the loadings (Table 9) show that the elements of the front and hind limbs, particularly MCL, MTL and RADL, account for much of the difference in elevation. The lower position of the NR male sample indicates that NR bison have longer limbs than AP bison. The high positive loadings of C7 and T1 indicate a vector for these variables in a direction approximately parallelling the major axes of the frequency ellipses. The position of the NR specimens relative to the two specimens of *athabascae* suggests that the two are similar with respect to the postcranial elements measured.

Table 9 Character loadings (correlation coefficients) of 25 postcranial variables on the first two principal components.

	I	II
1. SCAPL	0.984	0.118
2. SCAPW	0.969	0.144
3. HUML	0.998	-0.010
4. HUMW	0.959	0.140
5. RADL	0.979	-0.156
6. RADW1	0.959	-0.124
7. RADW2	0.988	-0.085
8. MCL	0.955	-0.253
9. MCW1	0.979	-0.098
10. MCW2	0.984	-0.079
11. FEML	0.988	-0.420
12. FEMW1	0.984	-0.026
13. FEMW2	0.988	-0.071
14. TIBL	0.984	0.006
15. TIBW1	0.988	-0.062
16. TIBW2	0.964	-0.095
17. MTL	0.955	-0.229
18. MTW1	0.984	-0.055
19. MTW2	0.984	-0.124
20. PELV	0.979	0.063
21. ILW	0.974	0.124
22. ACETW	0.988	0.056
23. ISCHW	0.935	0.210
24. C7	0.833	0.449
25. T1	0.935	0.282

Although only one plains female was available its position relative to the NR females suggests the differences observed in the males of both groups also hold true for the females.

The univariate statistics for the postcranial variables are listed in Table 10. NR males differ significantly from *athabascae* males in only one measurement (width of the ischium) (Table 9). The plains bison bulls, on the other hand, differ significantly from those of *athabascae* in 16 and from those of NR in 22 of the 23 variables (Table 10). The lower number of significant differences with *athabascae* is probably a result of small sample size of *athabascae*.

The best univariate discriminators as indicated by the probability of misidentification between NR and *B. b. bison* are MCL ($P \approx 0.05$); RADL ($P \approx 0.09$); RADW1 ($P \approx 0.10$); TIBL ($P \approx 0.10$); HUML ($P \approx 0.12$) and FEML ($P \approx 0.12$) with estimated percentages of joint-non-overlap ranging from 88 to 95%. In *athabascae* and *bison* the best univariate discriminators are MCL ($P \approx 0.01$); ISCHW ($P \approx 0.02$); TIBL ($P \approx 0.05$) and FEML ($P \approx 0.07$) with percentages of joint-non-overlap ranging from 83 to 99%.

Differences between NR and plains bison females (Table 11) were not tested because of small sample sizes. Examination of the means suggests however that the differences between the females are of the same magnitude as those observed between the males.

The mean size of different postcranial elements in NR males is from 3 to 23% greater than those of NR females, with an average of 12.6%. In the plains bison the means for the same measurements in males exceed those of females by 5 to 22% with an average of 12.8%. Sexual dimorphism of size of postcranial elements in both groups is thus quite similar.

Some of the postcranial variables were also compared in ratiodiagrams (Figures 27 and 28). The points for *B. b. athabascae* and NR bison show them to be highly similar to one another. Both differ from *B. b. bison* in size and in the proportions of certain postcranial elements, particularly those of the pelvic girdle (e.g. ISCHW).

Table 10 Means, standard deviations and observed ranges for 23 postcranial variables in adult bulls of *B. b. athabascae*, NR and *B. b. bison*.

	B. b. athabascae				NR				*B. b. bison*				*athabascae* vs NR	*t*-test NR vs *B. b. bison*	*athabascae* vs *B. b. bison*
	N	$\bar{x}$	SD	OR	N	$\bar{x}$	SD	OR	N	$\bar{x}$	SD	OR			
1. Scapula length	3	557.6	18.14	541–577	13	557.9	18.86	526–589	9	515.8	20.83	482–547	n.s.	4.9353[c]	3.0855[a]
2. Scapula, width	3	297.0	15.52	282–313	13	290.9	11.96	274–322	9	269.8	19.17	243–305	n.s.	3.1889[b]	n.s.
3. Humerus, length	2	404.0	12.72	395–413	13	404.5	13.47	386–427	9	367.7	18.30	325–392	n.s.	5.4461[c]	2.6135[a]
4. Humerus, width	2	57.5	0.71	57–58	13	57.2	2.36	49–61	9	50.0	4.63	41–54	n.s.	4.8299[c]	n.s.
5. Radius, length	3	361.0	15.13	344–373	13	370.0	11.67	349–396	10	336.9	12.62	316–350	n.s.	6.5109[c]	2.7921[a]
6. Radius, prox. width	3	109.3	3.21	107–113	12	111.0	4.08	106–117	10	98.5	5.58	85–106	n.s.	6.0410[c]	3.1226[b]
7. Radius, dist. width	3	98.3	4.04	94–102	13	99.8	4.40	92–106	10	91.4	6.21	76–97	n.s.	3.7974[b]	n.s.
8. Metacarpal length	3	228.3	5.50	222–232	13	226.3	6.50	210–236	10	208.3	4.07	200–214	n.s.	7.6774[c]	6.9708[c]
9. Metacarpal prox. width	3	82.0	1.73	80–83	13	81.4	3.12	75–86	9	74.5	5.29	64–83	n.s.	3.8833[c]	2.3465[a]
10. Metacarpal dist. width	3	80.6	1.52	79–82	13	81.2	4.04	77–93	9	77.8	1.37	76–79	n.s.	2.4573[a]	2.9972[a]
11. Femur, length	3	483.3	17.47	464–498	13	476.5	21.24	423–519	10	429.8	17.51	394–449	n.s.	5.8134[c]	4.6460[c]
12. Femur, prox. width	3	165.0	3.60	162–169	13	160.4	6.95	152–170	10	152.2	8.65	134–160	n.s.	2.5083[a]	2.4386[a]
13. Femur, dist. width	3	126.0	1.00	125–127	13	124.9	4.54	116–132	10	114.9	6.95	101–125	n.s.	4.1674[c]	2.6664[a]
14. Tibia, length	3	452.0	11.53	439–461	13	447.4	15.15	426–481	10	411.6	12.58	392–432	n.s.	6.0286[c]	4.9486[c]
15. Tibia, prox. width	3	129.3	2.08	127–131	13	128.8	4.04	123–139	10	124.2	5.43	118–134	n.s.	2.3437[a]	n.s.
16. Tibia, dist. width	3	81.0	2.64	79–84	13	81.1	2.66	78–86	10	75.6	4.72	65–82	n.s.	3.5275[b]	n.s.
17. Metatarsal length	3	275.6	5.13	270–280	13	272.4	12.88	238–287	9	256.3	7.89	246–270	n.s.	3.3283[b]	3.9013[b]
18. Metatarsal prox. width	3	63.6	3.05	61–67	13	63.1	2.75	57–69	9	60.8	3.07	57–67	n.s.	n.s.	n.s.
19. Metatarsal dist. width	3	73.0	2.00	71–75	13	72.3	2.27	70–79	9	68.9	1.55	67–72	n.s.	3.8833[c]	3.7276[b]
20. Pelvis, length	2	576.5	4.94	573–580	13	574.4	24.16	532–613	9	511.3	38.24	461–560	n.s.	4.7585[c]	2.3109[a]
21. Width of ilium	2	540.0	25.45	522–558	13	523.2	21.16	492–552	9	495.7	31.26	452–547	n.s.	2.4649[a]	n.s.
22. Width at acetabulum	2	298.0	2.82	296–300	13	284.5	12.27	261–302	9	272.8	9.33	263–289	n.s.	2.8382[a]	3.7547[b]
23. Width at ischium	2	337.5	13.43	328–347	13	301.9	17.66	273–326	9	263.8	18.55	235–294	2.6958[a]	4.8793[c]	5.7264[c]

[a] $P < .05$
[b] $P < .01$
[c] $P < .001$

The lengths of the neural spines of the cervical (C7), and all thoracic (T) and lumbar vertebrae (L) of small samples of adult specimens in which the epiphyses had fully fused also showed significant differences between the forms compared (Figures 29 and 30 and Table 12). The main differences are found in the last cervical and the first twelve thoracic vertebrae. The neural spines of NR and *athabascae* specimens exceed those of *bison* and *bonasus* in length in diminishing amounts from front to back. In the male samples, NR and *B. b. bison* differ significantly in neural spine length of the first to 12th vertebra (Table 12). The difference is greatest in the second thoracic vertebra with an estimated joint-non-overlap of 92%. The neural spines of adult females are shorter than those of the males, but the differences between the female samples are similar to those observed in the males, with NR and *athabascae* being very similar to one another and greatly exceeding *bison* and *bonasus* in the length of the last cervical and the anterior thoracic spines (Figure 30, Table 13). Because of small sample sizes in the females the differences between NR, *athabascae* and *bison* were not tested statistically.

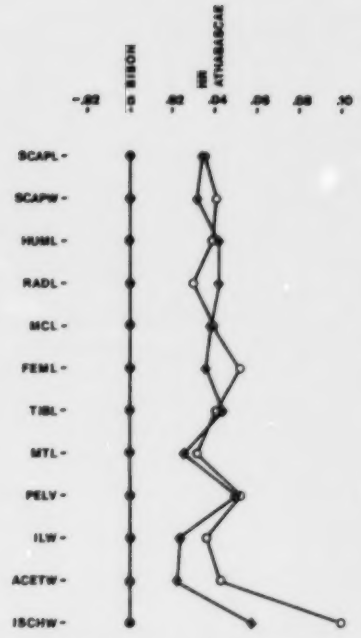


Figure 27. Ratiodiagram comparing 12 postcranial dimensions of adult males NR, *B. b. athabascae* and *B. b. bison*, with the latter serving as a standard.

Table 11 Means, standard deviations and observed ranges for 23 postcranial variables in adult cows of, NR and *B. b. bison*, and measurements of a single cow *B. b. athabascae*.

	B. b. athabascae(1)	NR				*B. b. bison*			
		N	$\bar{x}$	SD	OR	N	$\bar{x}$	SD	OR
1. Scapula length	465	5	459.1	14.82	456–478	3	417.8	5.63	413–424
2. Scapula width	232	4	224.8	5.87	219–233	3	205.3	9.29	195–213
3. Humerus, length	342	5	350.8	13.98	336–369	3	327.8	16.38	313–345
4. Humerus, width	44	5	43.3	2.53	40–47	3	42.3	2.08	40–44
5. Radius, length	314	5	332.1	13.69	324–356	2	308.0	22.62	292–324
6. Radius, proximal width	91	5	91.1	3.25	86–94	2	87.9	6.92	83–93
7. Radius, distal width	80	5	82.1	4.60	77–86	2	80.7	5.30	77–84
8. Metacarpal length	226	5	217.8	8.03	210–231	3	200.1	10.86	192–212
9. Metacarpal proximal width	67	5	65.1	2.06	63–68	3	63.3	1.52	62–65
10. Metacarpal distal width	65	5	67.2	1.40	65–69	3	65.6	3.78	63–70
11. Femur, length	—	6	419.2	14.75	404–445	2	390.0	39.59	362–418
12. Femur, proximal width	—	6	135.3	3.79	131–142	2	129.3	7.56	124–135
13. Femur, distal width	—	6	105.8	2.99	103–110	2	100.8	6.85	96–106
14. Tibia, length	393	6	401.4	13.07	390–425	3	366.6	21.82	353–396
15. Tibia, proximal width	109	6	111.3	3.42	107–117	3	110.6	6.65	103–115
16. Tibia, distal width	70	6	70.7	1.84	68–73	3	70.0	1.0	69–71
17. Metatarsal length	247	6	262.9	6.36	257–275	3	246.3	11.37	237–259
18. Metatarsal proximal width	52	6	53.3	1.69	52–56	3	53.6	1.52	52–55
19. Metatarsal distal width	60	6	62.3	1.23	60–64	3	59.3	2.30	58–62
20. Pelvis, length	484	5	477.3	11.67	458–487	1	416.0	—	—
21. Width of ilium	461	4	446.2	21.84	422–474	2	429.4	3.67	427–432
22. Width at acetabulum	253	6	247.4	7.60	235–254	2	238.0	7.07	233–243
23. Width at ischium	282	5	262.06	18.61	240–278	2	239.9	15.69	229–251

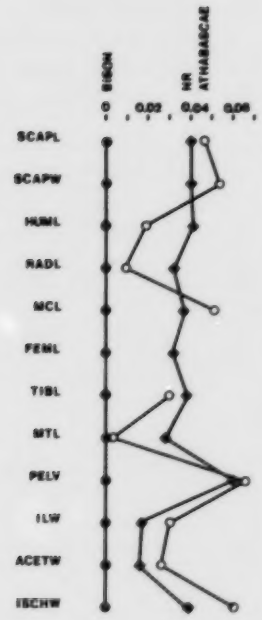


Figure 28. Ratiodiagram comparing 12 postcranial dimensions in adult female *athabascae*, NR and *B. b. bison*, with the latter serving as a standard.

f) Comparisons of external measurements and weights.

Three external measurements (TL, T, SHHT) and body weight of *athabascae*, NR and AP animals of both sexes were compared by PCA after log transformation (Figure 31). The NR and AP distributions show a relationship to one another similar to that previously observed in the CVA of postcranial variables.

Here again the major axis represents the trendline of increasing size and the difference in elevation between NR and AP distributions indicates a difference in proportion, with NR specimens having greater TL, T and SHHT than AP animals of similar size. The measurements for the single *athabascae* specimen (the Radford bull) were derived from the literature (Radford 1911, Soper 1941),[1] and may not have been taken precisely in the same way as in the others, but the proximity of this specimen to the NR specimens suggest their similarity.

[1] The length of tail cited by Soper (1941) appears to be erroneous. An extract of Radford's 1911 report in the Mammalogy Section files gives the length as 1' 7½".

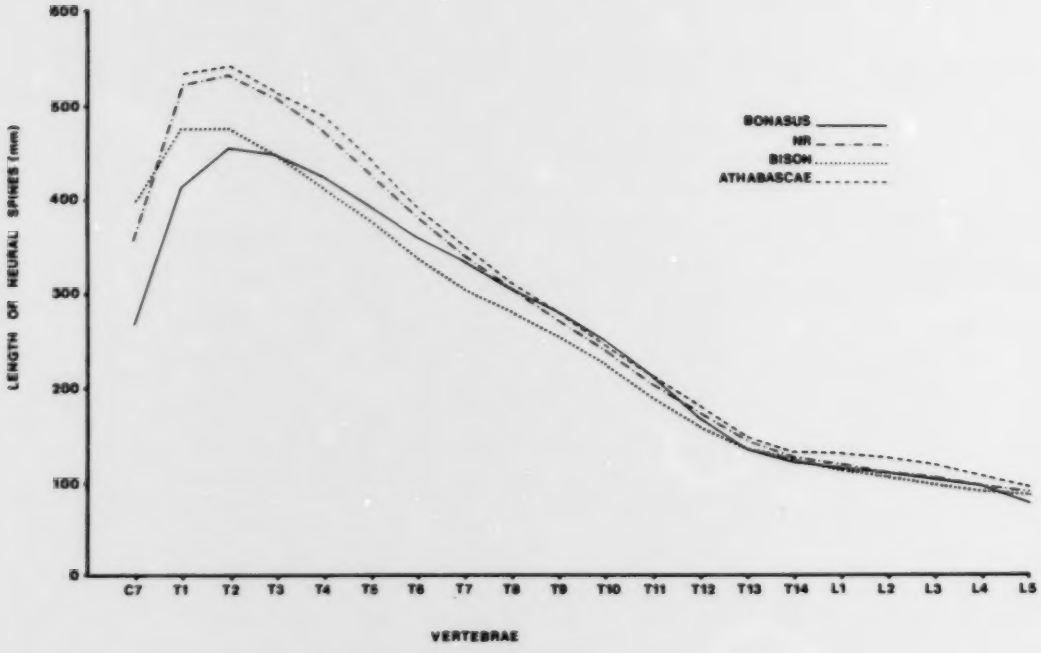


Figure 29. Mean lengths of neural spines in adult male bison; *B. b. bonasus* (N = 9) (data from Roskosz 1962): *B. b. bison* (N = 4); NR (N = 7) and *B. b. athabascae* (N = 1).

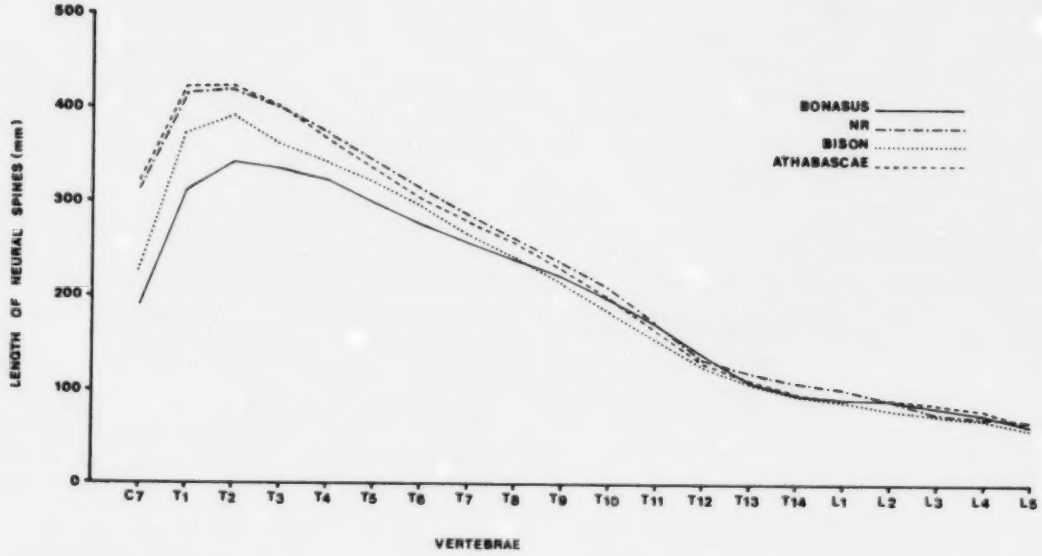


Figure 30. Mean lengths of neural spines in adult female bison. *B. b. bonasus* (N = 13) (data from Roskosz 1962): *B. b. bison* (N = 1); NR (N = 2); *B. b. athabascae* (N = 1).

Table 12 Greatest lengths of neural spines of the seventh cervical, the thoracic and the lumbar vertebrae of adult male bison.

	B. b. athabascae				NR				*B. b. bison*				*t*-test NR v. *B. b. bison*
	N	$\bar{x}$	SD	OR	N	$\bar{x}$	SD	OR	N	$\bar{x}$	SD	OR	
C7	3	421.7	6.35	418–429	7	354.7	24.26	307–383	4	391.0	34.18	352–434	n.s.
T1	4	547.0	13.66	533–565	7	520.4	22.36	483–544	4	474.1	20.17	457–501	3.4112[b]
T2	1	542.0			7	532.1	21.96	491–552	4	474.1	18.55	453–493	4.4306[b]
T3	1	514			7	505.8	20.49	468–527	3	444.6	26.53	419–472	4.0030[b]
T4	1	488			7	472.2	20.45	437–502	3	411.6	26.57	384–437	3.9666[b]
T5	1	441			7	428.0	23.79	388–465	4	376.0	20.83	351–402	3.6314[b]
T6	1	392			7	381.8	22.14	345–417	3	335.5	21.12	315–365	3.0651[b]
T7	1	350			7	340.1	18.61	310–367	3	303.0	19.14	286–330	2.8682[a]
T8	1	311			7	302.1	13.20	281–322	4	281.7	18.55	264–305	2.1420[a]
T9	1	277			7	272.4	10.21	253–283	4	253.5	17.91	236–278	2.2702[a]
T10	1	242			7	239.7	6.57	227–246	4	224.0	15.64	211–246	2.3848[a]
T11	1	210			7	204.2	4.82	196–210	4	188.7	10.43	179–202	3.4376[b]
T12	1	177			7	171.0	6.73	162–179	4	158.0	10.23	148–171	2.5710[a]
T13	1	143			7	142.8	6.12	135–150	4	134.7	8.80	126–145	n.s.
T14	1	132			7	125.0	6.19	116–135	4	123.0	7.25	116–133	n.s.
L1	1	130			7	117.8	7.17	111–128	4	114.2	6.13	108–122	n.s.
L2	1	126			7	108.0	6.16	101–120	4	102.7	6.13	94–107	n.s.
L3	1	118			7	101.0	6.55	95–114	4	95.5	5.06	88–99	n.s.
L4	1	—			7	94.2	7.65	87–110	4	89.2	5.67	81–94	n.s.
L5	1	95			7	86.2	7.31	81–100	4	81.5	5.19	74–86	n.s.

[a] $P < .05$
[b] $P < .01$

A similar comparison with two added measurements (RHT and HF) between AP and NR samples shows nearly identical results (Figure 32). NR adult males are situated largely (80%) outside the 95% confidence ellipse of AP males and are shown to be absolutely larger in overall size and to have relatively greater RHT, HF, TL and SHHT and to a lesser extent T than AP males.

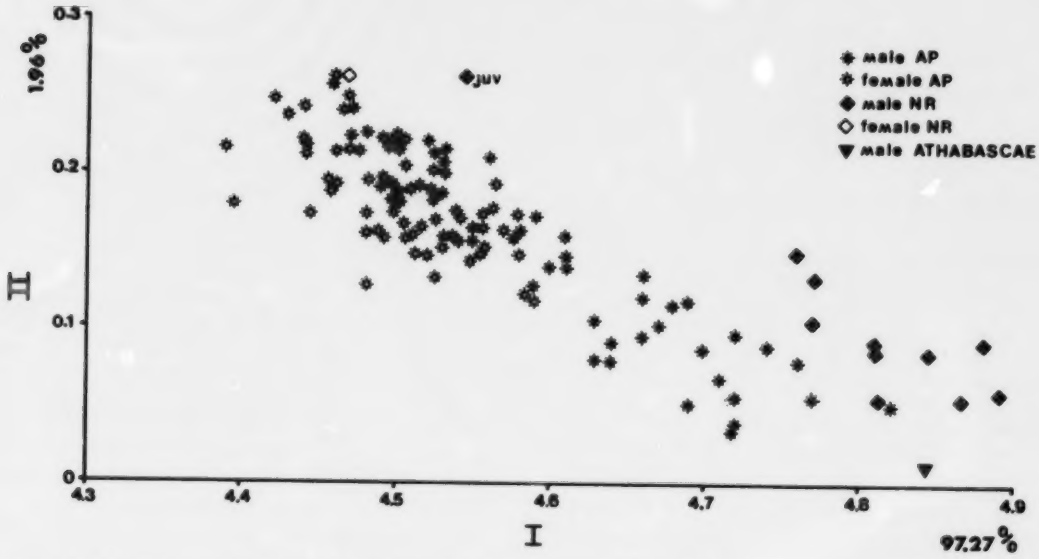


Figure 31. Relative position of specimens of AP, NR and *B. b. athabascae* in the projection on the first two principal components of a variance-covariance matrix of four characters (logarithms of three external measurements and body weight).

Table 13 Greatest length of neural spines of the seventh cervical, and the thoracic and the lumbar vertebrae of adult female bison.

	B. b. athabascae	NR				*B. b. bison*			
	(N = 1)	N	$\bar{x}$	SD	OR	N	$\bar{x}$	SD	OR
C7	322	1	310			1	224		
T1	422	2	415.5	7.77	410–421	2	375	1.41	374–376
T2	421	1	420.0			1	379		
T3	400	2	400.0	2.82	398–402	1	360		
T4	367	2	374.5	0.71	374–375	1	344		
T5	333	2	343.5	2.12	342–345	1	321		
T6	303	2	314.5	0.71	314–315	1	296		
T7	279	2	287.0	2.82	285–289	1	266		
T8	258	2	261.0	5.65	257–265	1	244		
T9	230	2	235.5	3.53	233–238	1	217		
T10	198	2	207.0	2.82	205–209	1	185		
T11	163	2	172.0	4.24	169–175	1	155		
T12	131	2	139.0	5.65	135–143	1	127		
T13	110	2	118.5	4.94	115–122	1	107		
T14	95	2	107.5	6.36	103–112	1	97		
L1	93	2	99.5	4.94	96–103	1	90		
L2	85	1	90.0			1	82		
L3	80	2	74.5	0.70	74–75	1	75		
L4	74	2	70.0	1.41	69–71	1	70		
L5	66	2	67.5	2.12	66–69	1	60		

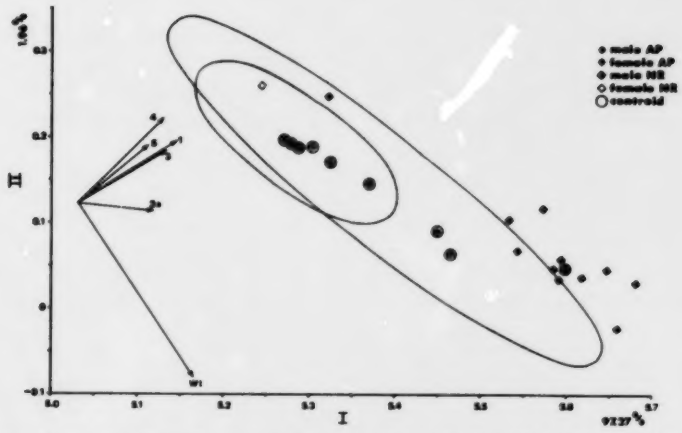


Figure 32. Relative position of centroids for different age classes of male and female AP and NR bison on the first two principal components of a variance-covariance matrix of six characters (Logarithms of five external measurements (1 TL; 2aT; 3 SHHT; 4 RHT; 6 HF;) and body weight (WT)). Individual specimens as well as the centroid for adult males are shown for the NR sample. AP bison are represented by centroids of different age groups and the 95% confidence ellipses for males and females. The major axis of the ellipse represents variation in size, with large specimens in the lower right hand corner of the graph and small ones in the upper left. Centroids of the AP sub-samples are from left to right: two-year-old cows; three-year-old cows; adult cows; four-year-old cows: two-year-old bulls: four-year-old bulls; adult bulls; old bulls. NR bison are represented by from left to right: a three-year-old cow; a two-year-old bull; ten adult bulls. The character vectors show the relative magnitude and direction of the contribution of the six variables to the principal components.

Comparison of the means for external measurements and weights show that NR and AP adults differ significantly in nearly all measurements (Table 14). NR bulls exceed AP bulls by 7 to 17% in the measurements compared and weigh on average 17% heavier. Estimated joint-non-overlap for the measurements compared exceeds 80% except for tail length (Table 14). The cows differ from one another in a similar way with NR exceeding AP by 6 to 11% in the measurements compared. Estimated joint-non-overlap in the cows exceeds 80% except for (Table 14). From the samples compared it appears that NR cows approximately equal AP bulls in some measurements.

Measurements and weights of AP bison are similar to those of plains bison from Wichita Mountains Wildlife Refuge (Halloran 1960). Comparison of T, HF, SHHT, and WT of adult AP bulls and 13 adult Wichita Mountains bulls (means T39.0; HF 59.96; SHHT 165.77; WT 589) showed significant differences in T ($t = 3.6920$ $P < .01$) and WT ($t = 5.0878$, $P < .001$). The means for the same variables of 14 Wichita Mountains cows 4½ years and older, all differed significantly from those of AP. In all cases the means of the Wichita Mountains cows were smaller (T 34; HF 55; SHHT 139.9; WT 382).

g) Comparison of outline shape and pelage characters.

The mean differences in standardized outline shape of adult plains, NR and European bison bulls and cows are shown in Figures 33 and 34. The most important differences in the profiles are in the lumbar area, the hump and the ventral contour of the head and neck.

Both North American forms differ from *B. b. bonasus* in the more sloping outline of the pelvic and lumbar region, which is nearly level in *bonasus*. The latter also shows a slight depression in the area of the neck in males (approx. 12 cm from the origin of the horizontal axis). NR bison differ from plains bison primarily in the shape of the hump, which reaches its highest point significantly farther forward in the former (Figure 33, 34). The highest point in the hump of the NR sample was 10.35 cm from the origin, in the standardized outline shapes compared to 8.85 cm in the plains male bison sample. The difference was highly significant ($t = 6.7259$ $P < .001$). A similar difference was found in the females with the mean for the highest point at 10.30 cm in NR and 8.82 cm in the plains females ($t = 2.1213$ $P < .05$). The anterior outline of the hump in NR bison descends more precipitously than in the others, giving the hump a characteristic angular appearance.

The differences in the humps of the three forms of bison are obviously related to the differences in the lengths of the neural spines discussed previously. Other factors such as musculature, posture and differences in skeletal proportions (Mohr 1939, Sokolov 1971) may contribute to the differ-

Table 14 Means, standard deviations, coefficients of variation, and observed ranges for five external measurements (cm) and body weight (kg) in adult NR and AP bison.

		NR ♂♂	AP ♂♂	*t* test	NR ♀♀	AP ♀♀	*t* test
HB	N	14	14	8.1042[b]	7	15	4.4179[b]
	$\bar{x}$	305.5	253.0		254.5	231.3	
	SD	13.81	19.92		21.86	6.16	
	CV	4.52	7.87		8.58	2.66	
	R	274-335	225-297		226-285	218-244	
T	N	14	14	3.7613[b]	7	15	n.s.
	$\bar{x}$	49.6	44.3		42.2	38.06	
	SD	3.20	4.19		3.81	4.78	
	CV	6.45	9.45		9.02	12.55	
	R	44-54	36-51		39-48	28-43	
Tail length incl., tassel	N	14			8		
	$\bar{x}$	84.2			69.2		
	SD	5.75			10.33		
	CV	6.82			14.92		
	R	75-95			55-91		
HF	N	14	14	6.0175[b]	6	15	4.5816[b]
	$\bar{x}$	66.3	61.5		61.5	57.7	
	SD	2.46	1.69		2.50	1.33	
	CV	3.71	2.74		4.06	2.30	
	R	62-71	58-64		59-66	56-60	
SHHT	N	14	14	5.0231[b]	7	15	6.9443[b]
	$\bar{x}$	182.2	165.5		162.2	146.6	
	SD	9.30	7.58		6.72	3.88	
	CV	5.10	4.58		4.14	2.64	
	R	168-201	152-179		155-172	140-152	
RHT	N	14	14	4.6712[b]	7	15	7.1518[b]
	$\bar{x}$	158.0	141.6		150.7	134.1	
	SD	11.65	6.07		7.15	3.85	
	CV	7.37	4.31		4.74	2.86	
	R	144-181	137-152		155-172	127-142	
WT	N	11	14	3.5441[a]	1	15	
	$\bar{x}$	943.6	792.5		508	497.6	
	SD	126.96	86.08			68.89	
	CV	13.45	10.86			13.84	
	R	759-1179	680-940			390-640	

[a] $P < .01$
[b] $P < .001$

ences in outline shape. The conspicuous neck bulge of *bonasus* bulls, which gives many of them a double-humped appearance, (also seen in many bison depicted in European paleolithic cave art), appears to result from the underlying muscles (acromiotrapezius, splenius and rhomboideus) gaining greater prominence because of the shorter neural spines of the last cervical and the first two thoracic vertebrae in this taxon. In North American bison the muscle bulge is obscured by the greater development of the neural spines. Mohr (1939, p. 447) gives an alternative explanation for the double hump of *B. b. bonasus* attributing it to the head being carried higher and thereby pushing the skin of the neck up to form a fold. The present analysis does not support this explanation. The differences in the dorsal outlines of the three bison are equally evident in both sexes, although the hump is more developed in the males. Aside from sexual dimorphism, age and to a lesser extent

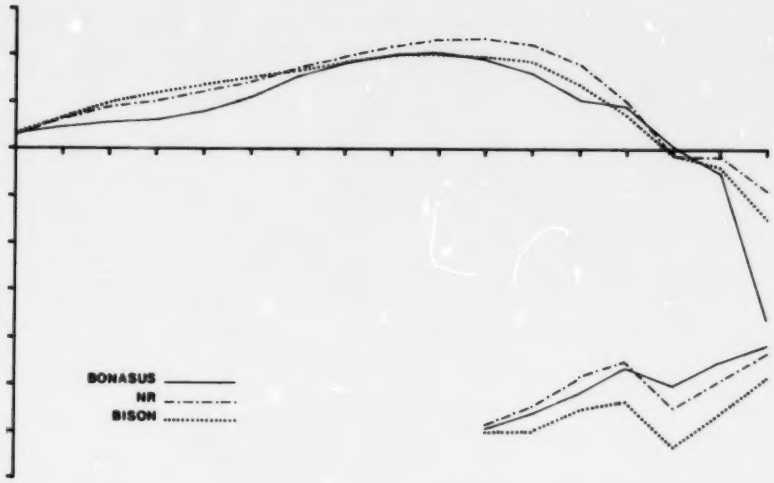


Figure 33. Mean outline shape of adult bulls based on standardized outlines of *B. b. bison* (N = 17), NR (N = 14) and *B. b. bonasus* (N = 6). Only the dorsal and anterior ventral outlines (beard and neck mane) are shown as it is these areas that show the differences among the different forms.

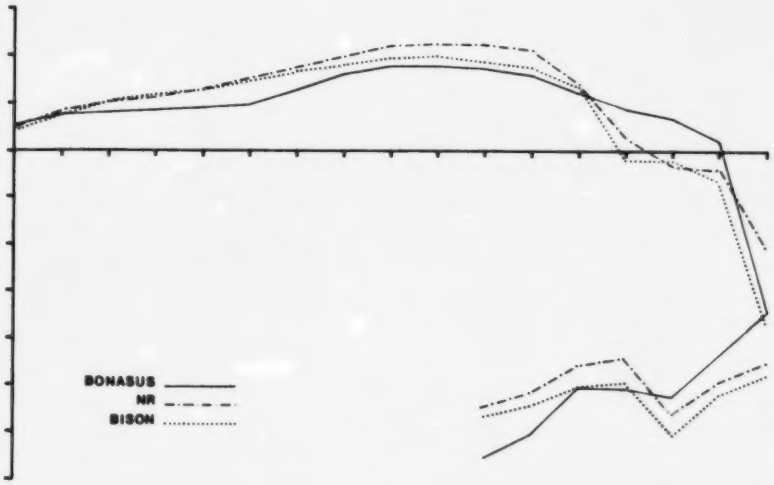


Figure 34. Mean outline shape of adult cows based on standardized outlines of *B. b. bison* (N = 10); NR (N = 9); and *B. b. bonasus* (N = 2).

seasonal variation affect outline shape. Seasonal differences in outline shape of NR bulls consist chiefly in the reduction, and in some cases the virtual disappearance of the preputial tuft. Although seasonal changes in pelage are evident, loss of display hair similar to that described for *B. b. bison* by Lott (1979) was not observed. Age variation has however, a marked effect on outline shape. Old adults, particularly in the males, have more developed humps and heavier more robust bodies than younger adults (Plate 1). The reasons for these differences lie in the greater length of the neural spines and greater muscular development of older bulls. The epiphyses of the neural spines are among the last to close. In *B. b. bonasus* epiphyseal fusion of the neural spines is reported to take place at age seven or shortly thereafter (Koch 1935). Although detailed studies of the chronology of epiphyseal fusion in North American bison are still lacking, it appears highly probable that it is similar to that in *B. b. bonasus* (Duffield 1973).

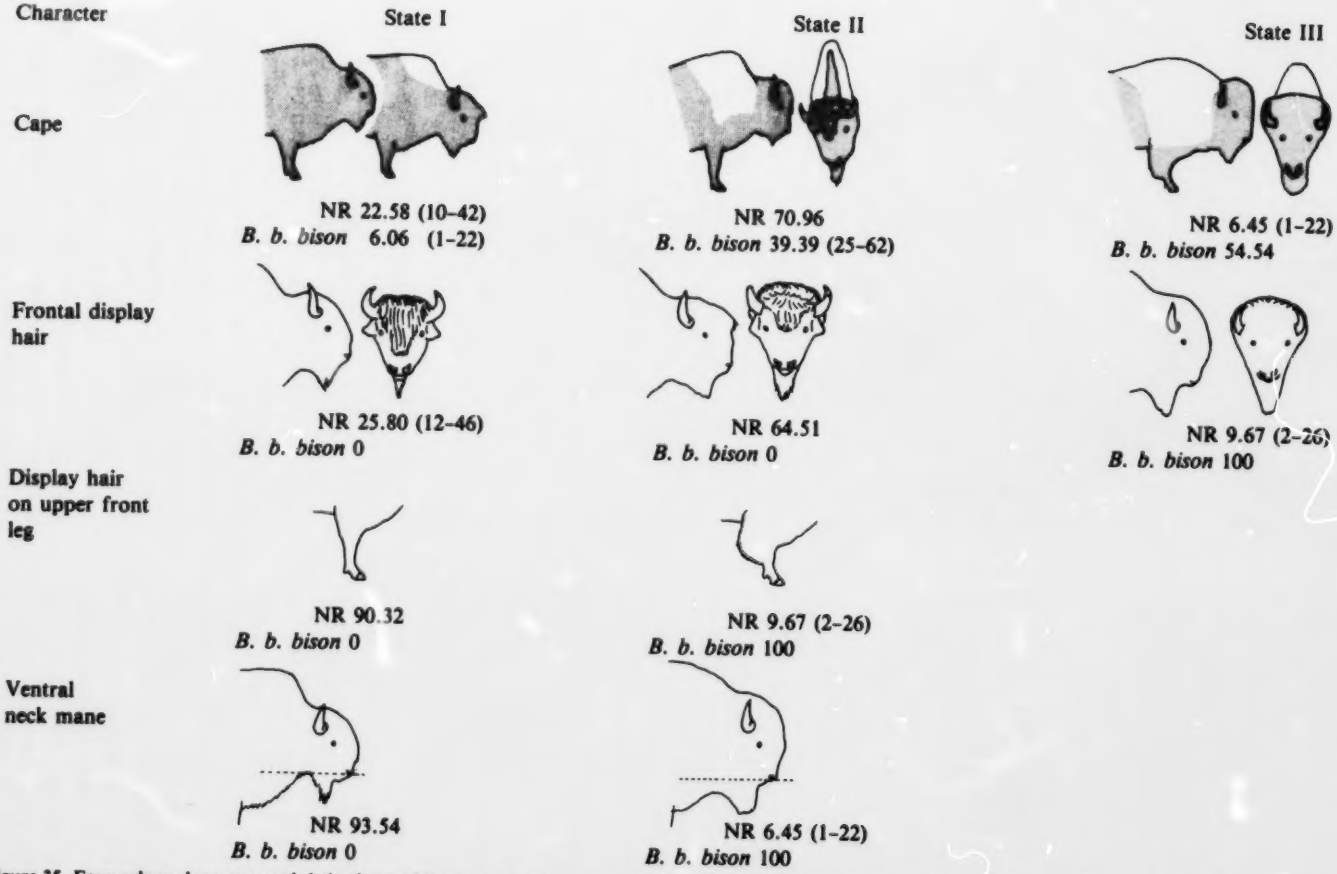


Figure 35. Four pelage characters and their observed frequencies of occurrence (%) in adult male NR bison (N = 31) and *B. b. bison* (N = 33). Where observed frequencies are less than 50%, the 95% confidence limits are shown in parentheses. The character states are characterized as follows: *Cape*. State 1. Colour of Cape approximately the same as that of the rest of the body or dorsally lighter (usually reddish brown) but lighter area not exceeding 25% of cape. State 2. Dorsal part of cape much lighter than body-light brown to blonde- and lighter area covering more than 25% of cape; dark median line present. State 3. Cape much lighter than body-light brown to blonde; light area covering more than 25% of Cape and no dark median line. *Frontal display hair*. State 1. Frontal display hair not well developed short to moderately long lying flat forward often in long strands, not filling space between the horns. State 2. Denser than in state 1, but flat and not filling space between horns, hair on nose may be erect. State 3. Frontal display hair well developed, long, dense and standing, forming a bonnet which fills space between horns.

Display hair on upper front leg. State 1. Short, not forming distinct "Chaps". State 2. Long, forming distinct "Chaps".

Ventral neck mane. State 1. Little developed in area of neck behind beard (which is usually thin and pointed), with outline at or above level of nose in normal standing position and making the neck appear more prominent. State 2. Well developed in area of neck behind beard (which is usually thick and blunt), with outline below level of nose in normal standing position obscuring the neck.

Ventrally, the outline shows the greater development of the beard in the North American bison, (particularly in *B. b. bison*) compared to *B. b. bonasus*. The neck mane in NR bison is generally less developed than is the case in *B. b. bison* and *B. b. bonasus*. The general effect of this is that the neck in adult NR bison tends to be more distinct. The ventral outline is thus determined by differences in hair length, which brings us to the analysis of pelage characters.

After preliminary exploratory evaluation of pelage characters in AP and NR bison, the number of characters selected for further analysis was reduced to four. The criterion for selection was the presence of two or more recognisable and definable character states that lent themselves to reasonably objective evaluation by an observer in the field or from good photographic images.

The four pelage characters selected and their states and their estimated frequency of occurrence in AP and NR populations are shown in Figure 35. Three of the four pelage characters (2, 3 and 4) show clear polarity of the character states between NR and *B. b. bison*, while the cape shows a greater degree of overlap.

My observations on pelage characteristics and dorsal outline of NR and AP bison generally agree with those of Geist and Karsten (1977) and Reynolds et al. (1982), but the distinctions listed by them are not always as clear cut as they lead us to believe and there are some discrepancies. My evaluation of some pelage characters listed by them was not conclusive because of inadequate data.

The differences in colour of the lower neck and the cape were not found to be as distinct as those authors suggest. Colour appeared to be quite variable in both NR and AP specimens and there was considerable overlap. However, light (blond) capes showing a clear cut demarcation appear to be characteristic of plains bison.

According to Geist and Karsten (1977) the preputial tuft of NR bulls appears to be shorter and thinner than those of AP bulls. I was not able to confirm this because I lacked measurements for AP bulls. Similarly tail length including the tassel could not be compared to evaluate Geist and Karsten's (1977) impression that the tail of NR bison was longer and hairier as no data were available for AP specimens. My observations indicate that these differences are not very great. Tail length is much more variable than other external measurements (Table 14). In both NR and AP bison the end of the tassel may reach the hock. However, in some prairie bison herds, presumably those with a greater admixture from southern stock, the tail may be noticeably reduced in length. NR and plains bison according to Geist and Karsten (1977) differ in that the contour of the back from the top of the hump to the root of the tail forms a descending line in the latter but not in the former. Outline shape comparison in the present study (Figure 33 and 34) showed NR and AP specimens to have similar descending dorsal outlines, but significant differences in the outline of the hump. Similarly, the outline shape comparison did not show any difference in the length of the neck of NR bison as suggested by Reynolds et al. (1982).

Geist and Karsten (1977) thought NR bison to be intermediate in pelage characteristics between wisent and prairie bison and postulated that juvenile pelage of NR bison would be intermediate in its characteristics between that of wisent and plains bison. One NR calf photographed on June 30, had a reddish juvenile pelage similar to that of the prairie bison and unlike the greyish brown juvenile pelage of the European bison. Some other calves observed in the latter half of August were largely dark but showed remnants of the reddish juvenile pelage. It appears, therefore, that NR bison resemble the prairie bison with respect to this character. Available data did not allow a detailed comparison of the juvenile pelages of NR and plains bison.

The same authors state that NR cows are less sexually dimorphic than plains cows, being closer to bulls in body size and proportions, as well as in horn form and pelage characteristics. They found NR cows on the whole more difficult to identify as cows. The analyses in the present study, however, have demonstrated that there is no appreciable difference in the degree of sexual dimorphism in NR and AP bison with respect to body size and proportions or horn form. As to pelage characteristics there is possibly a more pronounced sexual dimorphism in the development of display hair in AP bison. The greater difficulty in distinguishing the cows from bulls in NR bison is related chiefly to the female's greater overall size and high hump. As we have seen the body size-shape relationship in male and female bison is essentially the same, with centroids along a common axis (Figure 32). It follows from this that large cows tend to have a more bull-like appearance than small cows.

The differences in outline shape and pelage characters observed in NR bison in all probability reflect the character states typical of the original *athabascae*. Unfortunately, there is little information on the external appearance of the original *athabascae*, thus precluding a detailed comparison of the external pehnotypes of NR and *athabascae*. However, what little information does exist, confirms the above conclusions. The two photographs of a wood bison bull taken by Kitto (Graham 1923, Kitto 1924) show the characteristic hump outline seen in NR bulls. Seton (1927) commented on the absence of a mane, beard and "chaps" in the Radford bull (collected in December). The type specimen (NMC 299) (collected in March) likewise shows little development of the mane and beard and has no "chaps", and a sketch by Rowan (University of Alberta Archives), who collected two wood bison bulls in Wood Buffalo National Park in October 1925, shows similar character states. As two of the above specimens were collected in winter, it could be argued that wear caused the observed states. However, NR bison observed in Elk Island National Park, did not show great seasonal differences in outline shape. Seasonal differences consisted primarily of a lengthening of body hair and a conspicuous reduction in the prominence of the preputial tuft. It is likely that the effects of abrasion on the pelage would be most noticeable in late winter.

As to colour, the original *athabascae* is generally described as darker than the prairie bison (Seton 1886, McFarlane 1905, Graham 1923, Seibert 1925), but Mignault (Seton 1886) states that in summer the wood bison assumed a hue similar to that of the prairie bison.

Although, we may thus regard the present NR bison as close to original *athabascae*, we could expect certain plains bison traits to be evident on the basis of the previous osteological evidence. The frequency of occurrence of typical plains character states in the NR sample analysed appear to bear this out (Figure 35). The presence of chaps and plains bison type frontal display hair are of particular interest. Although hybridization experiments between North American and European bison and various other bovini have been conducted since the 1920's (Gray 1972), detailed information on the inheritance of certain traits is lacking. We do know, however, that in prairie bison-wisent F_1 hybrids, the prairie bison traits of chaps and frontal display hair dominate (Mohr 1952). We may assume that holds true also for plains-wood bison crosses. If these traits are determined by a single pair of alleles, as seems probable (Deakin et al. 1935), the frequency of the plains allele in the NR population, based on the estimated frequency of occurrence of the phenotypes in the population and the Hardy-Weinberg formula, would be about 0.05. If the above assumptions are correct, the allelic frequency would indicate the extent of possible introgression of the NR population by AP genes.

A weighted character index using four pelage characters and one outline shape character (the hump) was devised (Appendix 3) as a means of evaluating the external phenotypes in the field or from adequate photographic records. A sample of 33 AP and 32 NR adult bulls were scored. Of the AP sample 18 (54%) had scores from 90 - 100. 13 (39%) from 80 - 90 and 2 (6%) from 70 - 80. For NR bulls the scores were as follows: 9 (28%) had scores from 0 - 10; 20 (62.5%) from 10 - 20; one (3%) from 30 - 40 and two (6%) from 50 - 60. NR bulls with high scores are characterized by plains characteristics (Plate 1). The greater range of scores (0 - 60) in the NR sample indicates a high degree of variability possibly a result of introgression of *B. b. bison* genes.

Examples of variation in external characters observed in male and female NR bison are illustrated and compared to typical AP bison in Plates 1 to 4.

Plate 1. Photographs illustrating the range of phenotypic variation in NR bison bulls.

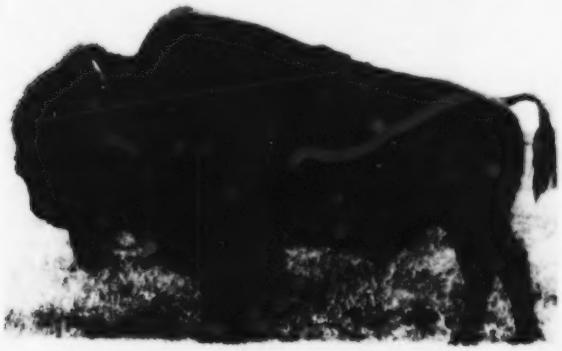
1. Fully adult NR bull showing a combination of external characters considered to be typical of *B. b. athabascae*. (character index score 0). Note the robust heavy body characteristic of fully mature males, the dark colour, procumbent and thin frontal display hair, thin beard, little developed ventral neck mane, lack of clear demarcation of the cape, lack of chaps, robust horns with slightly spirally twisted tips and dorsal outline with highest point far forward. Photo taken in Elk Island National Park, 28 July 1982, by Donna Naughton.

2. Full grown adult NR bull (character index score 10) showing a combination of characters similar to that of the previous bull, but having a somewhat lighter cape. Photo taken in Elk Island National Park, 3 October 1984, by Donna Naughton.

3. A younger NR bull (character index score 20) characterized by a less robust body and lower neural vertebral spines. Pelage characters and outline shape are those of *B. b. athabascae*. Photo taken in Elk Island National Park, August 1977, by David B. Campbell.

4. An even younger NR bull already showing the characteristic outline shape and procumbent frontal display hair. Photo taken in Elk Island National Park, 5 October 1984, by Donna Naughton.

Plate 1. Photographs illustrating the range of phenotypic variation in NR bison bulls.



5. Adult NR bull (character index score 40) showing a combination of plains (frontal display hair, chaps) and wood bison (hump) characteristics. Photo taken in the Moose Jaw Wild Animal Park, 17 June 1983, by H.W. Reynolds.

6. Adult NR bull showing some plains bison characteristics (chaps, relatively well developed frontal display hair, hump more like plains bison). Photo taken in the Metro Toronto Zoo, 3 September 1984, by C.G. van Zyll de Jong.

7. A younger NR bull from the same herd showing similar traits as well as a blond cape. Photo taken in the Metro Toronto Zoo, 3 September 1984, by C.G. van Zyll de Jong.

8. Adult male plains bison (AP) (character index score 100) showing the typical northern plains bison phenotype. Note dense standing frontal display hair, well developed ventral neck mane, chaps, light cape with clear posterior demarcation contrasting with dark head, dorsal outline ("carp back") and relatively thin simple horn. Photo taken in Waterton Lakes National Park, in late summer by J.C. Holroyd.

Plate 2. Phenotypic variation in NR bison bulls

1. Profile of adult NR bull (same individual as in Pl. 1, #1) showing typical procumbent frontal display hair, thin pointed beard, poorly developed neck mane and uniform dark cape. This individual in all likelihood embodies the pure primitive phenotype of the original *B. b. athabascae*. Photo taken in Elk Island National Park, 28 July 1982, by Donna Naughton.

2. A close up of the head of the same individual.

3. Adult NR bull, a somewhat smaller and probably younger animal than the bull in 1 and 2 but showing the same phenotype. Photo taken in Elk Island National Park, 28 July 1982, by Donna Naughton.

4. Close up of the same individual.

5. Adult NR bull with distinct plains bison phenotype (character index score 60). Note the dense erect frontal display hair, blond cape clearly set off from the rest of the body and simply curved thin horn. Photo taken in Wood Buffalo National Park, 10 September 1967, by E. Kuyt.

Plate 2. Phenotypic variation in NR bison bulls

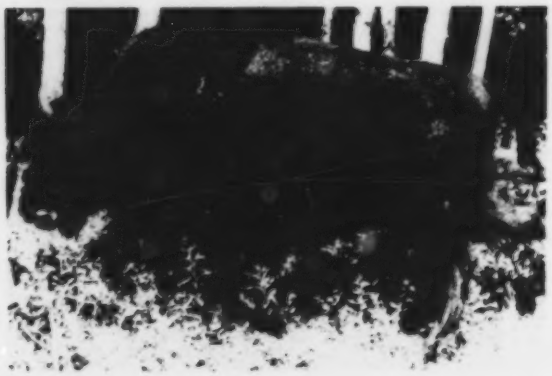
6. Head of an adult NR bull having phenotype similar to the animal in the previous picture. Photo taken in Elk Island National Park, 5 October 1984, by Donna Naughton.

7. Front view of the same NR bull as in fig. 3 and 4, representing the *athabascae* phenotype (character index score 0).

8. Front view of adult NR bull (character score 20) with somewhat more erect frontal display hair and lighter cape. Photo taken in Elk Island National Parks, August 1977, by David B. Campbell.

9. Front view of NR bull (character index score 40) with similar cape and frontal display hair confirmation as the bull in figure 8, but with heavy chaps. Photo taken in the Metro Toronto Zoo, 3 September 1984, by C.G. van Zyll de Jong.

Plate 3. Phenotypic variation in NR bison cows compared to AP cows.



1. Adult NR cow representing *athabascae* phenotype (character index score 0). Note lack of chaps, short sparse hair on head and dorsal outline. Photo taken in Elk Island National Park, August 1982, by Donna Naughton.

2. Adult NR cow showing similar phenotype. Photo taken in Elk Island National Park, 5 October 1984, by Donna Naughton.

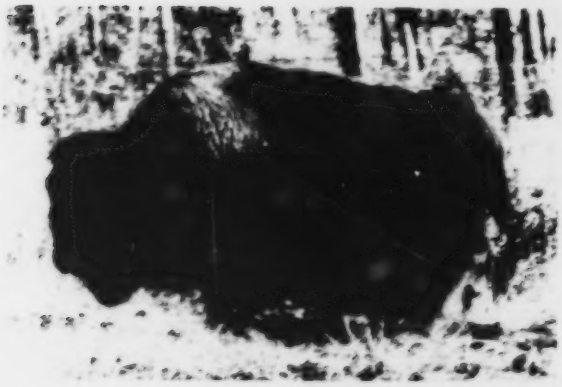
3. Adult NR cow with relatively well developed beard and ventral neck mane. Photo taken in Elk Island National Park, 5 October 1984, by Donna Naughton.

4. Adult NR cow with light cape and chaps. Photo taken in the Metro Toronto Zoo, 3 September 1984, by C.G. van Zyll de Jong.

Plate 3. Phenotypic variation in NR bison cows compared to AP cows.

5. NR cow with the characteristic forward *athabascae* hump. Photo taken in Elk Island National Park, October 5, 1984, by H.W. Reynolds.

6. NR heifer already showing characteristic forward hump. Photo taken in Elk Island National Park, 5 October 1984, by Jo-Anne Reynolds.



7. Adult plains bison cow (AP) showing characteristic "hair-roll", well developed beard and ventral neck mane, chaps and "carp" back. Photo taken in Elk Island National Park, 5 October 1984, by Donna Naughton.

8. Adult plains bison cow (AP) showing similar characters. Photo taken in Elk Island National Park, 5 October 1984, by Donna Naughton.

Plate 4. Phenotypic variation in NR bison cows compared to plains bison cows (AP).

1. Head of adult NR cow (the same individual as in Pl. 3 fig. 1). Showing short hair on the head and poorly developed beard and neck mane, characteristic of the *athabascae* phenotype.

2. Old adult NR cow, note procumbent frontal hair, short beard, clean legs and long right horn (left horn is broken). Photo taken in Elk Island National Park, 28 July 1982, by Donna Naughton.

3. Adult NR cow showing moderate amount of frontal hair and clean legs. Photo taken in Elk Island National Park, August 1977, by David B. Campbell.

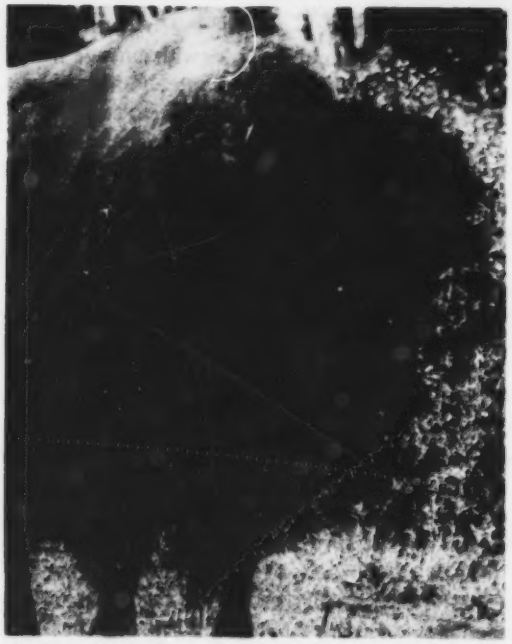
4. Face of adult NR cow showing short frontal hair and beard. Photo taken in the Metro Toronto Zoo, 3 September 1984, by C.G. van Zyll de Jong.

Plate 4. Phenotypic variation in NR bison cows compared to plains bison cows (AP).

5. Adult NR cow with relatively large amount of procumbent frontal hair, small beard, and forward hump. Photo taken in Elk Island National Park, 5 October 1984, by H.W. Reynolds.

6. Face of adult NR cow showing similar characteristics. Photo taken in Elk Island National Park, August 1977, by David B. Campbell.

7. Adult plains bison cow (AP) showing a well developed "hair roll" characteristic of most plains bison cows. Photo taken in Elk Island National Park, 5 October 1984, by Donna Naughton.



8. Adult plains bison cow (AP). Note the well developed frontal hair, beard and chaps. Photo taken in Elk Island National Park, August 1977, by David B. Campbell.

Conclusions and Discussion

1. Historical Geographic Variation and Subspeciation of North American Bison.

The preceding craniometric analyses of samples representing historical North American bison populations show that geographic variation was largely clinal in a predominantly south — north direction. However, a phenotypic discontinuity is revealed between boreal populations (*B. b. athabascae*) and plains populations (*B. b. bison*), coinciding approximately with the ecotone between grasslands and boreal forest in the northwestern part of the historical distributional range (Figure 10). This discontinuity, involving size as well as shape of the skull, fully justifies the recognition of the subspecies *B. b. bison* and *B. b. athabascae*. Evidence from analyses of postcranial morphology and external characters further supports the phenotypic discontinuity.

McDonald (1981) interpreted the differences between the two subspecies to be largely those of size, aside from some minor difference in horn core shape, and the transition between the subspecies merely as an increase in the slope of the north — south character size cline. However, of the change in six cranial variables with latitude shown graphically by him only two, spread of horn cores and horn core length along the upper curve, show a definite clinal change. The other four are probably not clinal. The change in limb characters (McDonald 1981), including humerus, radius and metacarpal length, are even less convincingly clinal. To the contrary, all show relatively little change between samples of plains bison and a considerable change between the northern plains population and *B. b. athabascae* suggesting a discontinuity rather than a cline.

Specimens from the Canadian Rocky Mountains, as well as those from areas west of the great plains in the United States are morphometrically close to those from the prairies. It is highly probable that prairie bison penetrated and crossed the mountain barrier through the predominantly east-west oriented river valleys and mountain passes. The montane and intermontane bison populations are thus considered to be *B. b. bison*. This conclusion agrees with that of McDonald (1981) and is contrary to that of Skinner and Kaisen (1947). The last mentioned authors included those populations in *B. b. athabascae* on the basis of larger measurements, and they postulated a dispersal route from the north through valleys between the Rocky Mountain ranges.

Cranial material from the southern Peace River region in Alberta and British Columbia analysed in this study, yielded somewhat ambiguous evidence as to the affinity of the historical bison population in that area. The analysis of six horn core and five cranial measurements of a small sample indicates near identity with the historical population on the Canadian prairies (Figure 6). The analysis of a different set of characters, comprising five cranial and two horn dimensions, resulted in a more intermediate position of the PR centroid, between plains bison and wood bison, although still considerably closer to the former (Figure 9). Finally, analysis of a much larger sample, but using only three variables, shifted the PR centroid closer to *athabascae* and away from *bison* (Figure 10). How are we to interpret these seemingly contradictory results? In my opinion the most likely explanation is that the population in the upper Peace River area was somewhat intermediate between *B. b. bison* and *B. b. athabascae*, but resembling the latter taxon more closely. The first two analyses, based on only five specimens, may not have adequately reflected variation in the upper Peace River populations. The larger sample used in the analysis of three variables, on the other hand, probably represents a more realistic picture. The area between the upper Peace River parklands and the prairies proper, consisting of heavily wooded country, constituted the transition zone between the two subspecies.

This conclusion is further supported by the information given to Seton (1886) by Elzear Mignault who lived in the Peace River area from 1863–75. According to Mignault the bison in the Peace River area were distinct from the prairie bison. He also implied that prairie bison occasionally penetrated the area, the last being killed in 1866. The area where the "prairie buffalo" was killed is not specified, although it is likely the observation was made in the valley of the upper Peace River.

Historical references to so called wood buffalo in Manitoba (Roe 1970) are not backed up by evidence from specimens. Here, as well as in other instances (see Roe 1970), we seem to be dealing with the uncritical application of the term "wood"

to plains bison observed in wooded country.

The historical distribution of *B. b. athabascae* was thus, on the basis of the objective evidence, restricted to the northwestern portion of the species' range (Figure 36), an area closely coinciding with that outlined by Soper (1941). The exact boundaries of the historical distributional range of *B. b. athabascae* cannot be determined at present on the basis of the available information. The distribution of specimen localities, localities given in historical reports and the distribution of toponyms relating to bison suggest the possible existence of a zone between the two taxa (Figure 36) that may have been only intermittently or sparsely populated.

Subfossil material referred to *B. b. athabascae* indicates a prehistoric range extending further north and west into the Yukon and Alaska (Figure 36). Three radiocarbon dates of 1350, 1465 and 1810 yrs BP for *B. b. athabascae* have been reported for the Yukon (Harington 1980a).

Two localities from which *B. b. athabascae* specimens have been reported, from near Fort McPherson on the Peel River (Skinner and Kaisen 1947, MacDonald 1981) and from western British Columbia (Smith 1977) are here rejected on grounds of morphometric and other evidence.

The Peel River locality is based on a partial cranium of an adult bull (USNM P 16861) collected by E.A. Preble in 1904. The discriminant score for this specimen (90.2) based on nine variables (Appendix 2) identifies it as a *B. b. bison*. The probability that the specimen was drawn from the same population as the *athabascae* reference sample is exceedingly small ($P < .0001$). A note by Preble attached to the specimen and not commented on by the authors previously named further undermines confidence in the origin of this specimen. The note reads as follows:

> "Bison skull obtained at Fort Simpson, Mackenzie, 1904 by Edward A. Preble.
>
> "This specimen was in one of the warehouses of the Hudson's Bay Company at Fort Simpson, having been saved probably because a sort of museum was for many years maintained there. The skull was stated by A.F. Camsell who had lived at that post for a number of years, to have been brought from Peel River (Fort McPherson). However in view of the fact that it bore no label and might have been confused in Mr. Camsell's mind with some other specimen it is quite possible that it really came from somewhere about Great Slave Lake, where the bison was common to within a comparatively recent date, and near which it still occurs. [signed] E.A.P.".

It seems highly probable that the skull was brought in from a locality much farther south than Preble suggested.

The skull from coastal British Columbia reported on by Smith (1977) was also identified by me as a *B. b. bison* on the basis of its published measurements. The unusual locality of the find, near Kitimat in the coast forest, moreover, casts doubt on the specimen's origin.

The proposed recognition of two subspecies in the plains bison (Krumbiegel 1980) is not supported by the results of the craniometric analyses. Reliable information on geographic variation in external characters of historical plains bison populations is sparse. Aside from some old photographic records, there appear to be no data that can be used in forming an idea of geographic and individual variation of external characters in historical prairie bison. A few old illustrations cannot be considered as an adequate foundation for the designation of a subspecies, as Krumbiegel (1980) has done. Moreover, it is reasonable to assume, given the continuous range across the Great Plains, that variation in pelage characters, like that of skeletal characters was clinal in nature. No useful purpose is served by taxonomically subdividing contiguous populations showing clinal variation.

2. Taxonomic Status of Extant North American and European Bison

The multivariate craniometric comparison of the two North American subspecies and the European bison lend support to the view that all living bison are conspecific (Bohlken 1967). The closer craniometric proximity of *B. b. bison* and *B. b. bonasus* to one another, than that of either to *B. b. athabascae* is difficult to harmonize with the view that the European bison is specifically distinct. The results of the craniometric analysis leaves us two options — either there are three species present or the scatter of the three groups represent intraspecific variation. Independent evidence from ecological and behavioural studies (e.g. Fuller 1960, Heptner et al. 1966, Krischke 1984, Lott 1974, 1979, McHugh 1958, Sokolov 1979) of American and European bison as well as the complete interfertility of the two favour the latter option. If one considers all available evidence, and one applies the criteria proposed by Mayr (1969 p. 197) to the question "subspecies or allopatric species?" one is led to conclude that

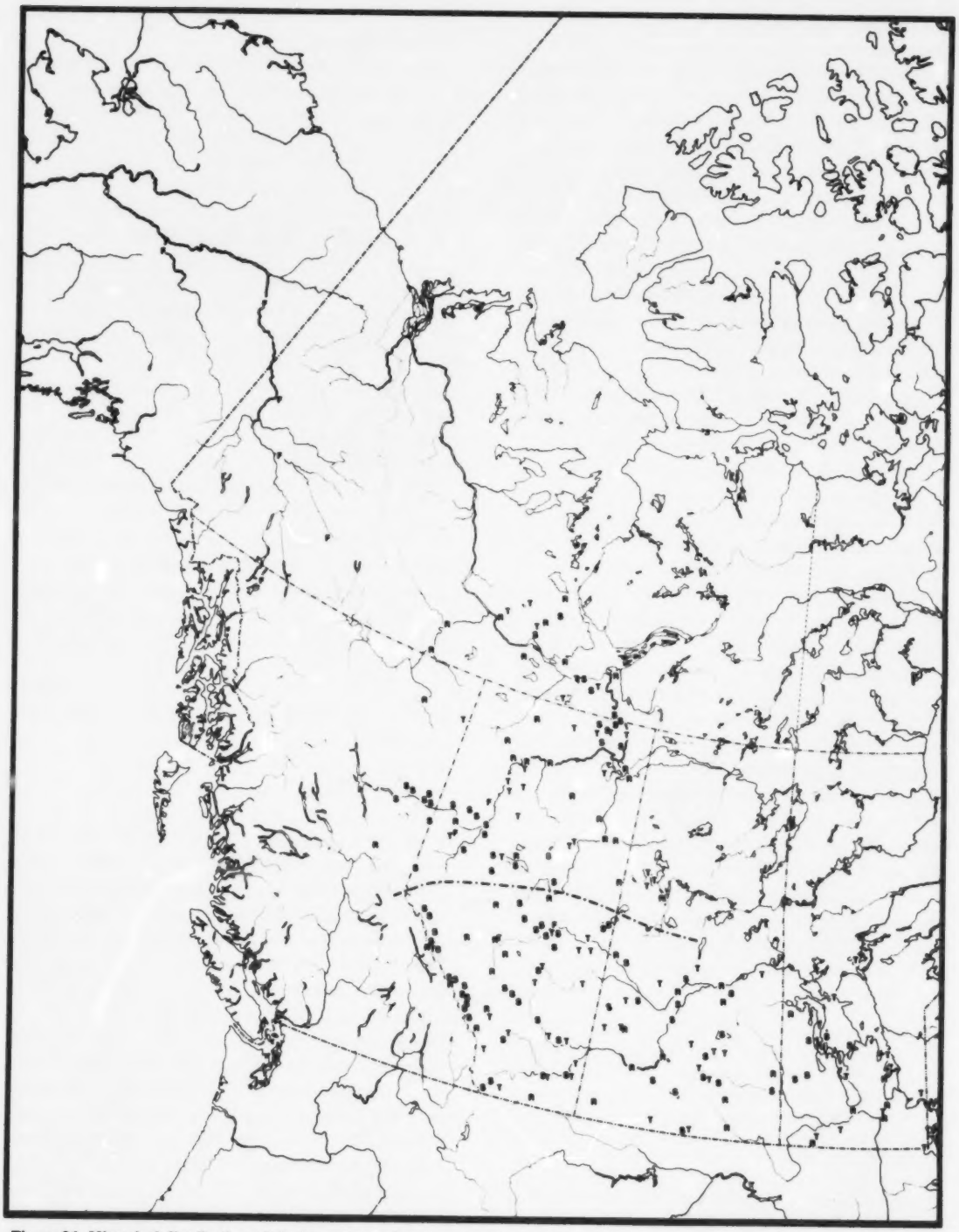


Figure 36. Historical distribution of the bison in northwestern North America based on specimen localities (S), historical reports (R), and toponyms (T), and showing the probable subspecific boundary between *B. b. bison* and *B. b. athabascae*. Localities where prehistoric bison referred to *B. b. athabascae* (F) have been found indicate the possible extent of the prehistoric distribution of this taxon.

American and European bison are subspecies of one species. Bohlken (1967), who compared the European bison and the American plains bison by means of univariate and bivariate techniques arrived at the same conclusion. I fully concur with his argumentation and taxonomic conclusions. Reluctance to accept conspecific status of the European and American bison is undoubtedly influenced by the marked phenotypic differences between them and their extreme disjunct historical distributions. These are, however, of relatively recent origin. The phenotypic differences displayed by modern forms of bison are, moreover, no greater than those observed in some other Holarctic species, e.g. *Cervus elaphus*, with similar late Pleistocene-Holocene distributions, and less than those found between the most divergent subspecies of *Syncerus caffer* (Grubb 1972). These examples illustrate the possible extent of variation within a species and show that the degree of difference among Recent bison is within the observed limits of intraspecific variation of related species.

3. Morphometric Relationships of Late Pleistocene-Holocene Bison and Subspecific Differentiation of North American Bison

The morphometric analysis of bison crania from the late Pleistocene and Holocene sheds some light on the possible origin and relationships of living forms. The comparisons show the well known progressive reduction in size (Holocene dwarfing Wilson 1980), as well as variation in the shape of the cranium and horn cores. An interesting observation that emerged from these analyses is that the variation within modern bison may be similar to that found within and between Holocene and late Pleistocene forms, as well as that between modern and earlier forms of bison. Viewed together in multivariate space they form one morphometric continuum, which is best regarded as representing one variable chronospecies. Thus late Pleistocene and Holocene bison from different parts of Eurasia were not unlike North American *occidentalis*, and the derivation of modern bison from a common stock as suggested by Skinner and Kaisen (1947), Fuller and Bayrock (1965) and Guthrie (1970, 1980) appears highly likely.

The presence of *athabascae*-like bison in eastern Siberia at the close of the last glaciation (Flerov pers. comm.) is particularly relevant to the question of the subsequent evolution of North American bison. This small-horned eastern Siberian bison is represented in the present analysis by measurements from a well-preserved skull from the Bol'shaya Chukochya River in the Kolyma River lowlands (Sher 1971). The similarity of this bison to North American *occidentalis* and to *athabascae* is strong evidence of the former existence of an ancestral Beringian population. After the reestablishment of the Bering Strait at the beginning of the Holocene, the Siberian population became extinct, probably during the Hypsithermal (Flerov 1979), but the American population survived and expanded southward. The disappearance of the ice barrier eventually led to contact and hybridization with the southern form (*B. b. antiquus*), as intergrades between the two indicate (Wilson 1975, Guthrie 1980, Harington 1984). The modern prairie bison (*B. b. bison*) probably evolved from this mixed stock during the Hypsithermal (about 7000–5000 BP) when extensive grasslands appeared (Harington 1984), and gradually increased its range as the grasslands expanded. At the same time woodland and parkland adapted forms (*occidentalis-athabascae*) were increasingly restricted to the northwestern parts of the species' range. Subsequent climatic, and possibly other factors as well, eventually resulted in contraction of *athabascae* range to its historical proportions (Figure 36). *B. b. athabascae* may be considered the more primitive of the two North American subspecies on the basis of its greater morphometric similarity to *B. b. occidentalis* and the retention of primitive external characters. Seton (1886) was the first to express the view that *athabascae* was the more primitive form, a view subsequently expressed or implied by Fuller and Bayrock (1965), and Harington (1984). *B. b. bison* on the other hand is morphometrically more remote from *B. b. occidentalis* and possesses more highly derived external characters (e.g. the high degree of development of display hair and chromatic variegation).

The results of the present analyses agree with the scenario outlined above i.e. 1) the conspecificity of Eurasian and North American Holocene bison, 2) the dual origin of modern North American bison from a Beringian element (*B. b. occidentalis*) and an earlier Nearctic line (*B. b. antiquus*), and 3) subsequent evolution of a grassland-adapted form (*B. b. bison*) and a more conservative parkland form (*B. b. athabascae*), retaining more of the ancestral characters.

Contrary to the interpretation of other North American investigators (e.g. Skinner and Kaisen 1947, Guthrie 1970, Fuller and Bayrock 1965,

Wilson 1975), McDonald (1981) postulated a phylogenesis of modern North American bison from an autochthonous Nearctic line (*B. antiquus*, of his classification) which he believes may also have given rise to *B. b. bonasus*. Flerov (1979) stands apart from both schools of thought, deriving *bonasus* and *athabascae* from Palearctic *priscus*, and *bison* from the Nearctic autochthon *antiquus*. As to the origin of *B. b. athabascae*, McDonald (1981) suggests two alternatives. Body size could have been 1) retained from the ancestor (his *B. antiquus*) or 2) resulted from more recent adaptive differentiation from *B. b. bison*. He regards the second alternative as probably "more important over time in influencing the nature of *B. b. athabascae*" (McDonald 1981, p. 261). As we have seen in the preceding analyses more than just size is involved. *B. b. athabascae* differs from *B. b. bison* (and resembles *B. b. occidentalis*) in a number of characters other than size, which we may assume to be genetically determined. Considering all these characters together, the view that *B. b. athabascae* is a direct and little differentiated descendant of *B. b. occidentalis* is more probably correct.

4. The Nature and Maintenance of Subspecific Differences in North American Bison

As noted in the introduction some regard the differences between *B. b. athabascae* and *B. b. bison* "as but a superficial divergence springing from environment" (Soper 1941: p. 375). The idea that the observed differences between wood and plains bison are a result of environmental induction is not new and still finds its adherents. It is difficult to separate ecophenotypic variation from that under genetic control, without resorting to experimental study of the effects of environmental variables on morphology. There are, however, a few lines of evidence that shed light on the question of whether we are dealing with ecophenotypic or genetic variation.

1. NR bison were transplanted from their original habitat to the Mackenzie Bison Reserve in 1963 and to Elk Island National Park in 1965, two very different environments. Specimens obtained 14 years later from Elk Island National Park and 19 years later from the Mackenzie Bison Reserve did not differ appreciably from one another, nor did they differ appreciably from those specimens collected at the original sites in Wood Buffalo National Park. Moreover, NR bison from Elk Island National Park do not show to this day any evidence of approaching the plains bison from Elk Island National Park north of the highway, in the morphological characters evaluated, although both herds exist under nearly identical environmental conditions. These observations suggest genetic rather than ecophenotypic variation.

2. The morphometric similarity of NR specimens, drawn from three widely spaced localities, to those of *B. b. athabascae* and *B. b. occidentalis* (samples separated in time and space) also suggest genetic control rather than environmental induction of the observed differences. Likewise, the morphometric similarity of AP bison to historic plains bison, the former living under very different conditions than its ancestors, leads to the same conclusion.

3. One can gain some insight into the plasticity of the bison phenotype by considering the effects of captivity. Plains bison have been kept in zoos for many generations. None of the characters assessed as characterizing the plains bison has been altered significantly — except perhaps for size and weight. Captive animals free from stress and on a high plane of nutrition, may attain larger size and greater weight than their wild counterparts. For example, a breeding bull of the Catskill Game Farm weighed 1035 kg at age 12 (Heck 1968). That weight greatly exceeded the upper limits observed in herds living under semi-natural conditions in the Wichita Mountains Wildlife Reserve (Halloran 1960) and in Elk Island National Park. We are again led to the conclusion that the characters which distinguish wood bison from plains bison are genetically controlled, are not ecophenotypic variations, and constitute good subspecific characters.

Subspecific distinctness was probably maintained by a combination of ecological and behavioral factors as well as by natural selection.

1. Ecological factors minimized interbreeding between the two subspecies, because populations were largely spatially isolated by unfavorable habitats. The distribution of *B. b. athabascae* within their range was probably highly clumped, with demes centered in areas of favorable habitat and absent from areas of unsuitable habitat (e.g. muskeg). An intervening belt of heavy boreal forest acted as a natural barrier to contact with *B. b. bison* to the south. The barrier, although not impenetrable, must have at least minimized contact. The distribution of *B. b. bison* populations was probably less clumped because of the more

continuous nature of suitable habitat.

2. Behavioral factors minimized interbreeding, because different traditions tended to separate populations during the reproductive season. Bison demes tend to occupy relatively restricted home ranges of which they possess intimate knowledge with regard to resources and their seasonal availability. This leads to seasonal movements from certain parts of the home range to others. These seasonal movements are regular and tend to remain stable as long as no major climatic or other environmental changes disrupt them. The presence of long established and well worn bison trails used by generations of bison testify to this (Soper 1941). Evidence for such seasonal movements in *B. b. bison* populations occupying the Canadian prairies is presented by Moodie and Ray (1976) and Morgan (1980). They documented annual movements into the boreal parklands in winter and back to the prairies in spring and summer. Seasonal movements from winter ranges to summer ranges and back are also known from Wood Buffalo National Park (Soper 1941) and Yellowstone National Park (Meagher 1973). Free ranging European bison, as well, are reported to move seasonally (Heptner et al. 1966, Baskin 1979). I have no information on the seasonal movements of historical populations of *B. b. athabascae*, but we may assume that they did not behave differently from free-ranging bison today. Their summer ranges were probably remote from those of the nearest plains bison. If so, there would have been little or no contact between the two subspecies during the breeding season; an effective barrier to gene flow.

3. Differential directional selection, imposed by the diverse habitats of the two subspecies may have played a role in maintaining allele frequencies and phenotypic distinctness. Unlike environments can exert a strong selective pressures on natural populations. The resulting genetic differentiation in adjoining populations may confer a greater degree of fitness to each, allowing them to survive better under the respective specific environmental conditions of the different habitats. The different selective regimes would thus offset any effects of gene flow that may occur.

The interaction among ecological and behavioral factors, gene flow and natural selection could thus account for the maintenance of the distinctness of *B. b. bison* and *B. b. athabascae*. Similar mechanisms still operate and can be analyzed in other large ungulates, like caribou, (e.g. *Rangifer tarandus caribou, R. t. groenlandicus* and *R. t. pearyi*) which occupy heterogeneous environments and have developed very different traditions in response to them.

McDonald (1981) suggests that hunting by Indians, which according to him appeared to have taken place primarily along the margins of the main range, may have been the most influential factor separating the *athabascae* and *bison* gene pools by preventing the peripheral expansion of the range of *B. b. bison*. It is difficult to conceive how this could have been achieved given the human population densities, which must have been quite low in early historic time, and the state of contemporary hunting technology. Probably human predation in early historic time could not have presented a significant barrier to expansion.

5. Taxonomic Status of Present Remnant Populations in Canada.

Craniometric comparison of AP bison with historical populations of *B. bison* show them to be highly similar to historical populations from the Canadian prairies. In pelage characters and outline shape AP bison also resemble historical Canadian prairie bison, as a comparison with photographs of an original bison bull (Anonymous 1906, Lothian 1981) from the Canadian prairies showed. The close resemblance of AP bison to historical bison from the Canadian prairies is not altogether surprising. The origin of the AP herd can be traced to stock from the area near the Alberta-Montana border and Saskatchewan with some admixture of southern stock (Texas, New Mexico, Kansas and Nebraska) (Dary 1974, Lothian 1981).

The multivariate morphometric analyses of skeletal characters and the comparison of pelage characters and outline shape of NR specimens with those of *B. b. athabascae* (insofar as sufficient information on homologous characters was available) and *B. b. bison* (AP) specimens show them to be somewhat intermediate, but much closer to *B. b. athabascae*. The morphological evidence thus suggests that some gene flow occurred between the population in the Nyarling-Buffalo Lake area and populations elsewhere in the park, with *B. b. bison* genes in their gene pools. Phenotypic similarity cannot be translated into precise genetic terms. Morphometric analysis for example measures the effects of many gene loci, but how many alleles are responsible for the observed

divergence is not known. To complicate the picture further, non-genetic sources of variation often contribute to the results. It is therefore difficult to evaluate the degree of hybridization that may have occurred. If the differences in the expression of frontal display hair and chaps are based on a one-locus, two-allele system as suggested earlier, the pelage-character analysis suggests a possible admixture of AP genes of approximately 5%.

The conclusion that gene flow occurred is contrary to the original assumption of isolation by distance and intervening "inhospitable and unproductive terrain" (Banfield and Novakowski 1960). Circumstantial evidence from other sources suggests that the isolation was less than complete. Soper (1941) stated that the country between the Ninishith Hills and the upper Buffalo River and the Caribou Mountains is swampy, except for some sandy ridges, inaccessible in summer and shunned by bison in winter. However, he mentions and illustrates a bison trail which followed the Ninishith Hills northwest to the Nyarling River. Soper's informant, Sousi Marie, stated that he saw Wainwright bison as far north as the Klewi River as early as 1929 and "that trails, progressively dimmer, exist . . . . to the Nyarling." Harington (1977) reports an observation by L.P.E. Choquette, of trails connecting the Nyarling River area with the range of mixed herds, confirming the information given by Soper (1941). The presence of brucellosis and tuberculosis in the Nyarling herd (Novakowski and Stevens 1965) — diseases believed to have been introduced into Wood Buffalo National Park from Wainwright — also point to contact.

It is unfortunate that too few specimens from herds occupying different areas of Wood Buffalo National Park were available for this study. A morphometric analysis of such material would help to interpret the impact of the introductions of plains bison on the phenotypic variation of the different demes inside and outside the Park.

If the population estimate of 1500 *B. b. athabascae* in 1922 was correct (Graham 1923), the greater abundance of *B. b. bison* in the population in the late 1920s (6673) suggests a proportionately larger contribution to the genetic make up of the present population in Wood Buffalo National Park. However, two factors may have influenced the degree and extent of hybridization, the demographic composition of the population of the two taxa and the extent of movement among demes. Most of the introduced plains bison were female and young (mostly yearlings and two-year-olds, only 332 were three-year-olds). It is therefore probable that during the first few years following the initial introductions, *athabascae* bulls were primarily involved in breeding. If this was the case, the genetic contribution by *B. b. athabascae* would be greater than the gross figures would suggest. Release sites of the introduced plains bison were all located along the eastern park boundary below the confluence of the Peace and Slave rivers. Depending on the extent of movement and exchange of individuals among different local populations, hybridization may have affected different herds (e.g. Lake Claire, Hay Camp and Grand Detour herds) to varying extents. If movement between demes was limited, the Hay Camp and Lake Claire Herd would be expected to show the greatest similarity to AP stock. Further work is needed to shed light on these problems.

A comparison of blood characteristics of NR bison with those of five different herds of plains bison (Peden and Kraay 1979) showed that differences among the plains bison herds were at least as great as those between NR bison and some of the plains herds. The relationship among herds based on frequencies of red blood cell antigens are not congruent with those based on morphology, and did not provide evidence for the subspecific distinction. As most of the present herds originated from small founder populations, the founder effect may have had an important influence on the observed frequencies. The lack of agreement between morphology and red blood cell antigens reflects the fact that different character sets may represent different adaptations (assuming that observed differences have adaptive significance) subject to different selection pressures. Blood groups may not have evolved at the same rate as morphology, as the high degree of similarity of cattle and bison with respect to blood groups appears to indicate. Each of the nine blood group systems found in cattle has a known homologue in bison (Stormont et al. 1961). Blood group frequencies can be altered relatively easily within a species judging from the divergent frequencies found in different breeds of cattle. Morphology of the body as a whole, on the other hand, appears to be linked to the basic ground plan of a species, which is probably under complex polygenic control and less subject to rapid change.

Karyotypes of NR and plains bison were found to be identical (Ying and Peden 1977), and highly similar to that of the European bison (Orlov

and Chudinovskaya 1979). All possess a complement of 60 chromosomes. The only difference between European and American bison is in the Y chromosome, which is submetacentric in the former and usually acrocentric in the latter. Variation from submetacentric to acrocentric Y chromosomes appears to be present in American bison (Wurster and Benirschke 1968, Hsu and Benirschke 1969, Ying and Peden 1977), but there is no information on the frequency of occurrence of the two types. The karyotypes of *Bison* and *Bos* are highly similar (Orlov and Chudinovskaya 1979), representing thus another character set of low interspecific divergence.

The results of the present analyses demonstrate the close proximity of NR bison to the original *B. b. athabascae*, and warrant their inclusion in that taxon, in spite of the apparent slight introgression of *B. b. bison* (AP) genes. The WBNP populations could be designated as intergrades (*B. b. bison* × *athabascae*) until they can be analysed in greater detail.

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Appendix 1

List of specimens used

Samples representing remnant populations

B. b. bison AP males (total 93) — *Alberta* — Elk Island National Park (*NMC* 6010, 21895, 27504, 27508, 27510, 27511, 45416, 51387, 51389, 51395; *UCY* S1, S2, S5, S7, S8, S9, S11, S12, S13, S15, S16, S17, S18, S19, S21, S22, S24, S27, S29, S32, S33, S34, S38, S40, S41, S44, S45, S46, S48, S49, S51, S52, S55, S56, S59, S61, S63, S64, S66, S68, S70, S72, S74, S75, S77, S78, S79, S80, S82, S84, S86, S87, S90, S92, S94, S95, S98, S99, S101, S102, S103, S106, S108, S110, S111, S118, S125, S126, S127, S128, S130, S131, S132, S133, S134, S135, S136, S142, S146, S147). Buffalo National Park, Wainwright (NMC 5552). *Manitoba* — Riding Mountain National Park (MMMN 8055, 8554).

AP females (total 52) — *Alberta* — Elk Island National Park (*NMC* 6009, 27502, 27503, 27505, 27507, 51388, 51390, 51391, 51392, 51393, 51394, *PMA* 66-3-2, 69-35-1, *UAMP* K980-12, *UCY* S6, S10, S23, S25, S26, S28, S30, S39, S42, S43, S47, S51, S53, S57, S67, S69, S76, S81, S83, S85, S88, S93, S96, S97, S109, S110, S114, S115, S120, S121, S122, S129, S137, S138, S140, S141, S143, S145).

B. b. bison × *B. b. athabascae* — *WBNP* males (total 11) — *Alberta* — Wood Buffalo National Park, Grand Detour (CWS Edmonton, unnumbered), Government Hay Camp (*USNM* 263390), Pine Lake (*USSC* 2330), Lake St. Clair (*NMC* 48087, 48089, 48091, 48092, 48093, 48096, 48099, 48100).

WBNP Females (total 13) — *Alberta* — Wood Buffalo National Park, Sweetgrass (*NMC* 51399, 51400, 51401, 51428), Murdock Creek (*NMC* 12091), Lake St. Clair (*NMC* 48084, 48085, 48086, 48088, 48090, 48095, 48097, 48098).

B. bison ssp? — *SE* males (total 6) — *Alberta* — Wood Buffalo National Park (*AMNH* 86950). Wood Buffalo National Park, Salt River (*AMNH* 130171), Salt Lick, 5 Acre Wallow (*AMNH* 98953), 16 km from Slave River (*AMNH* 98228, 98229), Salt Plain (*AMNH* 98958).

SE females (total 3) — *Alberta* — Wood Buffalo National Park, Salt Plains (*AMNH* 98954, 98957, 98959).

B. b. athabascae — *NR* males (total 35) — *Alberta* — Elk Island National Park (*NMC* p. 32628, *NMC* 45622, 45623, 45624, 45625, 45626, 45627, 45628, 45629, 45630, 45631, 45632, 51371, 51374, 51402, 51422, 51423, 51424, *PMA* 73.82.1, 74.86.1, 75.23.1. *Northwest Territories* — Wood Buffalo National Park, Needle Lake area (*NMC* 24026, 24027, 39875, 51376, 51377, 51378, 51379, 51380), Copp Lake (*NMC* 51403); Mackenzie Bison Sanctuary (*NMC* 51408, 51409, 51412, 51413, 51417).

NR females (total 19) — *Alberta* — Elk Island National Park (NMC 51372, 51405, 51406, 51407, 51425). *Northwest Territories* — Wood Buffalo National Park, Frying Pan Lake (*NMC* 24028), Needle Lake area (*NMC* 39876, 51381, 51382, 51383, 51384, 51385, 51386, 51427); Mackenzie Bison Sanctuary (*NMC* 51410, 51411, 51414, 51415, 51416).

B. b. bonasus — males (total 23) — *BM(NH)* 45.10.13.2, 1946.12.17.1; *BZM* 8030, 20466, 22072, 22077, 33832, 33833, 33824, 33863, 41709, 44213, 46548, 91474, *ZMA* 1400, 1404, 5290.16.037, 18.404; *Wien* 1311, 1558, 2765, 5536, 7056.

Females (total 11) — *BM(NH)* 92.3.15.2; *BZM* 8032, 14798, 22078, 33837, 33838, 45287; *IH* 4623; *MMMN* 8596, 1937.153; *ZMA* 1335.

B. b. caucasicus — males (total 4) — *BZM* 33861; *Wien* 1594, 1596, 2320.

Females (total 2) — *BZM* 41673; *Wien* 2322.

Samples representing historical populations

B. b. athabascae — males (total 19) — *Alaska* — valley of Tanana River (*USNM* 223292). *Alberta*: Wood Buffalo National Park (*AMNH* 73615, *PMA* 68-31-1, 68-31-2, 68-31-4, *UAMZ* p626); near Fort Smith (*NMC* 4538) west of Fort Smith (*USNM* 177632); Lying Wood Mountain (*NMC* 625); 80.5 km SW of Smith Landing (*USNM* 172689); between Athabasca and Great Slave Lake (*MCZ* 24017); Wood Buffalo National Park, Salt Prairie (*NMC* 8755), Murdock Creek, (*NMC* 11436), Blind Bull Lake (*NMC* 11435). *Northwest Territories*: Great Slave Lake (*AMNH* 18163, *MCZ* 21933); 80.5 km SW Fort Resolution (*NMC* 299); near Fort Providence (*USNM* 177630); Yukon: Pelly River near Selkirk (*USNM* 5513).

Females (total 1) — *Alberta*: Pine Lake, Wood Buffalo National Park (*NMC* 10405).

B. b. bison — *CP* males (total 58) — *Alberta* — Drumheller (*NMC* 1803, *PMA* 80-10-1); junction of Bow and Belly Rivers (*NMC* 5591); Little Sandhill Creek near Red Deer River (*NMC* 5592); Beaver Crossing (*NMC* 51373); Trout Creek (*UCY* A: 05-825); Big Hill Springs (*UCY* A(G); Jenkin Buffalo Jump (*UCY* A (I)); S. of Spruce Grove (Alta. Beach Mus. unnumbered) Alexander Indian Res. (Alta. Beach Mus. unnumbered); Alberta Beach (Alta. Beach Mus. unnumbered); Fort Assiniboine (Barrhead Mus. unnumbered); Pembina Flats (Sangudo Mus. 3 unnumbered); W. side Cooking Lake (Tofield Mus. unnumbered); 9.7 km W. Tofield (Tofield Mus. 2 unnumbered); Beaverhill Lake (Tofield Mus. unnumbered); Buffalo Lake, 7 km SE Bashaw (priv. coll.); Medicine Hat (priv. coll.); Sundre (priv. coll.); Fort Saskatchewan (priv. coll.); South Ghost River (priv. coll.); Bonnyville (priv. coll.); Hairy Hill (priv. coll.). *Manitoba*: near Lake Winnipegosis (*NMC* 9564); Gypsumville (*MMMN* 8073); McArthur Lake, Riding Mountain National Park (*NMC* 33386). *Saskatchewan*: (*NMC* 10345); bank of South Saskatchewan River near Saskatoon (*US* 2299); near Chaplin (*NMC* 9565); S. of Battleford (*NMC* 9566, 9567); near Prince Albert (*NMC* 8833); Old Wives Lake (*NMC* 51426, *UCY* AC(J)); shore Last Mountain Lake near Silton (*SMNH* p632); NW of Regina (*SMNH* p537); Killdeer (*SMNH* 10922); between Bolney and Maidstone (*PMA* 79-26-1); Osler (17 priv. coll. unnumbered).

CRM males (total 53) — *Alberta*: Between Red Deer and Panther River S of Yaha Tinda Ranch (*NMC* 33395); Yaha Tinda Ranch (*NMC* 33372, 33363); Buffalo Lakes (*NMC* 33355); Bowden (*NMC* 33361); Smoky River (*NMC* 33393); Banff National Park, Stoney Creek (*NMC* 33365); Red Deer River, 12.9 km W Scotch Camp (*NMC* 33354, 33384); Baker Creek (*NMC* 33378), Panther River (*NMC* 33385), Tyrrell Creek Flats (*NMC* 33399), Tyrrell Creek (*NMC* 33371), Indian Head Warden Station (*NMC* 33389), Glacier Lake (*NMC* 33379), Bow River, 8 km W of Banff (*NMC* 33391), 9.7 km S of Dormer Cabin (*NMC* 33370), 19.3 km up Spray River (*NMC* 51396); Jasper National Park, Sulphur Springs (*NMC* 33358), Brazeau District (*NMC* 33356, 33374, 33390), Brazeau Falls (*NMC* 33357), Jasper Park Lodge (*NMC* 33406), Moosehorn River (*NMC* 33376), Maligne Lake (*NMC* 33377), Isaac Creek (*NMC* 33362), lower end Maligne Range (*NMC* 33381), Willow Creek (*NMC* 33368, 33375); Waterton Lakes National Park (*NMC* 33360, 33366, 33401, 33405, 36173, 51397, 51398); Waterton Lakes National Park, Twin Butte (priv. coll. 3 unnumbered), Spring Creek Hatchery (*NMC* 33340, 33392), N Fork Trail Creek (*NMC* 33364), Canyon Creek Church Camp (*NMC* 51370), Pass Creek Flats (*NMC* 33403), north side Trail Creek (*NMC* 33359), Horseshoe Basin (*NMC* 33398), mouth of Pass Creek (*NMC* 33397, 33380), Waterton River (*NMC* 33404, 33396), Indian Creek Badlands (*NMC* 33382, 33402).

CRM females (total 4) — *Alberta*: Mount Sarbach, Banff National Park (*NMC* 33388); Jasper National Park (*NMC* 33373); Jasper National Park (*NMC* 33367), Willow Creek (*NMC* 33369).

PR males (total 24) — *Alberta*: Kinuso (*NMC* 51375); Manning (*NMC* 51418, 51419); 16 km N DeBolt (DeBolt Mus. unnumbered); Brownvale (Brownvale Mus. unnumbered). Eureka River, 48.3 km NW Fairview (Fairview Mus. unnumbered); N of Enilda (High Prairie Mus. X38); W of Triangle (High Prairie Mus. X40-1-2); 38.6 km S of High Prairie (High Prairie Mus. X56), High Prairie area (High Prairie Mus. X63); 1.6 km N of Enilda (High Prairie Mus. 973-101); 9.7 km S of town of Peace River (Pioneer Mus. 73-557); 80.5 km from town of Peace River (Pioneer Mus. Grand Prairie 20); Wabasca (priv. coll.) Spirit River (priv. coll.); 24.1 km WNW Brownvale (priv. coll.), Calling Lake (pers. comm. N. Novakowski). *British Columbia*: Fort St. John area (*BCPM* 2794, priv. coll. unnumbered); Upper Cache Creek (*NMC* 51420, priv. coll. unnumbered); Pouce Coupé River, 16 km NE Dawson Creek (Dawson Creek Mus. unnumbered); Hudson Hope area (Hudson Hope Mus. unnumbered); Rose Prairie (priv. coll.).

PR females (total 1) — *Alberta* Torrens Towers (*PMA* 69-93-1).

CGP males (total 45) — *Montana: AMNH* 5475, 5476, 5480, 130208, 130209, 16300, 16301, 16303, 16305, 16306, 16307, 16308, 16311, 16313, 16314, 16315, 16317, 16318, 16321, *MCZ* 8377, 34083, *USNM* 17632, 22664, 22665, 22667, 122667, 122669, 122670, 122673, 122674, 122676, 122677, 122688, 122689, 122693, 122695, 122699, 233520, 243298, 274791, 300324. *Wyoming: MCZ* 1215, 1216, 1218, 7895.

CGP females (total 22) — *Kansas: MCZ* 105. *Montana: AMNH* 130210, 130211, 130212, 16322, 16323, *USNM* 2841, 2842, 38302, 38306, 122669, 122672, 122685, 179087, 300324. *South Dakota: AMNH* SD-2180, SD-2181, SD-2182, SD-2183, SD-2184. *Wyoming: MCZ* 1217, *UWYO* 3081.

USRM males (total 16) — *Colorado: DMNHC* 1846, *USGS* A. *Montana: UM* G0295, *USNM* 120507, 120512, 221089. *Oregon: USNM* 246529, 249842, 249844, 249846, 249894, 249895, 250092. *Utah: USNM* 1442. *Wyoming: AMNH* 139937, *USNM* 168816.

USRM females (total 13) — *Oregon: USNM* 249841, 249843, 249845, 249847, 249848, 249849, 249850, 250089, 250090, 250091, 250093, 250094, 250095.

SGP males (total 15) — *New Mexico: USNM* P(A). *Oklahoma: TMM* A. *Texas: PPHM* B, C, D, F, 630a, 76 2-1, 915-a, 1173-1, 1482-1, *TMM* 139, *TTU* A13212, *USNM* 126620, 126621.

EUS males (total 2) — *Kentucky: MCZ* 2047, 2050.

Samples representing earlier Holocene and late Pleistocene populations

B. b. occidentalis — males (total 43) — *Alaska: USNM* p4157. *Alberta: NMC* 12442, 17530; *PMA* p81-42-1, p68-2-150, p68-2-164, p68-2-195, p-68-2-624, p-69-17-19, p74-16-2; Fort Saskatchewan priv. coll. 2 unnumbered; near Calgary priv. coll. unnumbered; Banff Archives, unnumbered, pers. comm. C.R. Harington (1984); Fort Saskatchewan priv. coll. unnumbered; Pioneer Mus. Grande Prairie 18, 1; Spirit River *NMC* 51421; *Iowa: ISUMZ* 38959; *SMP* 21-67-2, 43-51-2, 155-56-2, 156-56-2 (A). *Manitoba: NMC* 2813. *Minnesota: MMNH* 198, 450, 723, 738, *USNM* p10541, p10545. *Nebraska: FMNH* p26249. *North Dakota: NDSU* G166. *Saskatchewan: SMNH* p1240a, p1240c. *South Dakota: ISUMZ* p199. *Texas: DMNHT* 629, *TMM* 725, *TTU* A1975/18. *Wisconsin: MMNH* 603A, 603E. *Yukon: MNC* p2242, 1733, *USNM* p5513.

Females (total 6) — *Alberta: PMA* p68-2-148. *Minnesota: SMM* p67-1-34. *Wyoming: UWYO* NC2560, p69-20-1. *California: LACM* RLB913, RLB1007.

B. b. antiquus — males (total 4) — *Alberta: NMC* p12442, *PMA* p69-20-1 — *California: LACM* RLB913, RLB1007.

Females (total 6) — *California: CM* 10195, *LACM* HC1245, 1246, 1255, *YPM* 10602 — *Minnesota: USNM* p10544.

B. b. priscus — males (total 3) — *Alaska: AMNH* A685-3249, *AMNH* AFAM30623, *AMNH* AFAM46885.

Other: Eastern Siberia — Moscow Pal. Mus. 835-624-39 (male), *Netherlands — ZMA* 4388 (male).

Appendix 2 Discrimination of Crania of Adult Male *B. b. bison* and *B. b. athabascae* Discriminant Function Analyses Using Different Numbers of Variables

Using nine characters

Character	Discriminant Weights	*athabascae* (N = 12) character means	*bison* (N = 75) character means	Score contribution to distance (D^2)
VD	0.391508	94.06	74.47	7.668
TD	0.090249	98.72	79.15	1.766
WHCO	0.201389	295.67	265.35	6.105
OC	0.179051	186.17	151.51	6.205
CW	-0.110337	127.38	123.66	-0.410
CLLC	0.073058	292.67	241.96	3.705
TB	-0.093566	213.17	179.07	-3.191
GPW	-0.051882	358.00	320.03	-1.978
SHTT	0.000866	700.75	604.57	0.083

Dividing point between groups 98.046*

athabascae
centroid 108.027

range 98.270 - 114.749

bison
centroid 88.066

range 78.448 - 98.219

D^2 *athabascae — bison* 19.961

Standardized normal deviate 2.233

Probability of incorrectly assigning an unknown specimen ≈ 0.01

* The dividing point is shifted from the mid point toward the less numerous group by an amount equal to (log R)/D, R is the ratio of the more numerous to the less numerous group (Davies 1971).

Using eight characters

Character	Discriminant Weights	*athabascae* (N = 12) character means	*bison* (N = 74) character means	Score contribution to distance (D^2)
VD	0.485495	94.06	74.47	9.443
TD	0.010876	98.72	79.39	0.210
WHCO	0.099340	295.67	266.22	2.926
OC	0.117815	186.17	153.28	3.874
CW	-0.109679	127.38	123.82	-0.389
CLLC	0.092826	292.67	241.20	4.777
TB	-0.107834	213.17	180.36	-3.537
GPW	0.050245	358.00	321.50	1.834

Dividing point between groups 96.767

athabascae centroid 106.241
range 98.522 - 113.075

bison centroid 87.104
range 76.112 - 99.227

D^2 *athabascae — bison* 19.137

Standardized normal deviate 2.187

Probability of incorrectly assigning an unknown specimen ≈ 0.01

Using seven characters

Character	Discriminant Weights	*athabascae* (N = 12) character means	*bison* (N = 75) character means	Score contribution to distance (D^2)
VD	0.510904	94.06	74.68	9.900
TD	0.018877	98.72	79.35	0.366
WHCO	0.137628	295.67	266.33	4.037
OC	0.129480	186.17	153.13	4.277
CW	-0.119818	127.38	123.81	-0.427
CLLC	0.090518	292.67	240.99	4.678
TB	-0.111933	213.17	180.45	-3.662

Dividing point between groups		92.595
athabascae	centroid	102.084
	range	93.454 - 108.753
bison	centroid	82.914
	range	73.065 - 95.103
D^2 *athabascae* — *bison*		19.170
Standardized normal deviate		2.189

Probability of incorrectly assigning an unknown specimen ≈ 0.01

Using five characters

Character	Discriminant Weights	*athabascae* (N = 12) character means	*bison* (N = 88) character means	Score contribution to distance (D^2)
VD	0.318622	94.06	74.48	6.239
TD	0.058985	98.72	79.30	1.146
WHCO	0.107565	295.67	266.06	3.185
OC	0.142588	186.17	152.17	4.847
CW	-0.071918	127.38	123.72	-0.263

Dividing point between groups		77.534
athabascae	centroid	84.979
	range	76.810 - 91.577
bison	centroid	69.826
	range	61.312 - 83.542
D^2 *athabascae* — *bison*		15.154
Standardized normal deviate		1.946

Probability of incorrect identification of an unknown specimen ≈ 0.02

Using four characters

Character	Discriminant Weights	*athabascae* (N = 12) character means	*bison* (N = 75) character means	Score contribution to distance (D^2)
VD	0.407611	94.06	75.13	7.714
TD	-0.014046	98.72	79.79	-0.266
WHCO	0.064110	295.67	267.64	1.797
OC	0.099538	186.17	154.05	3.196

Dividing point between groups		68.365
athabascae	centroid	74.439
	range	66.506 - 79.884
bison	centroid	61.997
	range	53.495 - 71.960
D^2 *athabascae* — *bison*		12.441
Standardized normal deviate		1.764

Probability of incorrect identification of an unknown specimen ≈ 0.04

Using three characters

Character	Discriminant Weights	*athabascae* (N = 12) character means	*bison* (N = 97) character means	Score contribution to distance (D^2)
VD	0.464413	94.06	74.62	9.028
TD	-0.050373	98.72	79.43	-0.971
WHCO	0.126151	295.67	266.74	3.649

Dividing point between groups		70.275
athabascae	centroid	76.000
	range	68.637 - 81.091
bison	centroid	64.302
	range	57.825 - 73.413
D^2 *athabascae* — *bison*		11.698
Standardized normal deviate		1.710

Probability of incorrect identification of an unknown specimen ≈ 0.04

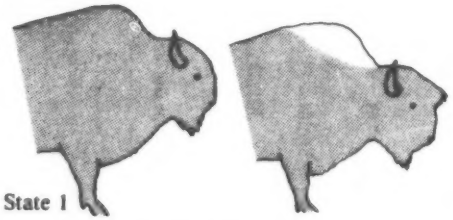
Appendix 3 Character index for evaluating external phenotypes of adult male and female North American Bison.

The animals to be scored should be in prime pelage (late summer-fall) to reduce the effects of bleaching abrasion and growth of winter pelt.

CHARACTER INDEX NORTH AMERICAN BISON ADULT BULLS

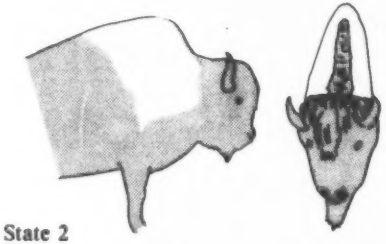
CHARACTER

1 Cape



State 1

Colour of cape approximately the same as the rest of the body or dorsally lighter (reddish brown), lighter area up to 25% of cape 0



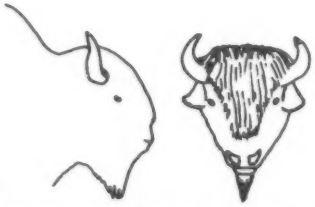
State 2

Much lighter than body, light brown to blond, lighter area covering >25% of cape; dark medial line, bisecting lighter areas of cape present 0.5

State 3

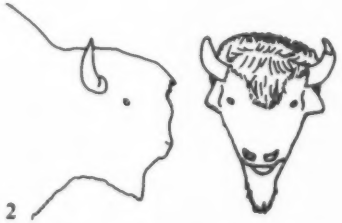
Much lighter than body, light brown to blond covering >25% of cape, dark medial line, absent 1

2 Frontal display hair



State 1

Not well developed, short to moderately long, lying flat forward, often in long strands, not filling space between horns 0



State 2

Denser than in 1, but flat and not filling space between horns; hair on nose may be erect 0.5

State 3

Well developed, hair very long and dense, standing forming a "bonnet" filling space between horns 1

3 Display hair on upper front leg

State 1

Short (< 10 cm), not forming distinct "cuffs" or "chaps" 0

State 2

Long (up to 50 cm) forming distinct "cuffs" or "chaps" 1

4 Ventral neck mane

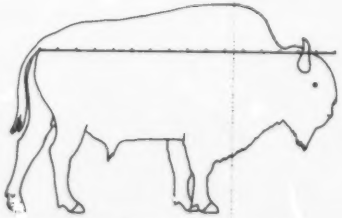
State 1

Little developed in area of neck, behind beard at or above level of nose in normal standing position; beard usually thin and pointed 0

State 2

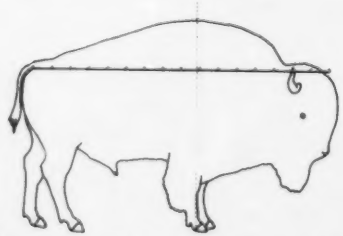
Well developed, in area of neck, behind beard below level of nose in normal standing position; beard usually full and rounded 1

5 Hump



State 1

Highest point of hump anterior, between points 10 and 11, anterior slope to neck precipitous 0



State 2

Highest point of hump posterior, at point 9, anterior slope to neck generally more gradual 1

TOTAL

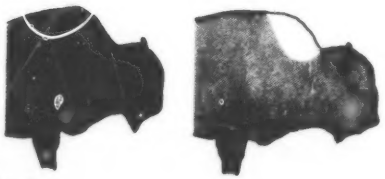
$$\frac{\text{TOTAL}}{5} \times 100 = \square$$

SCORE

B. b. athabascae 0 50 100 *B. b. bison*

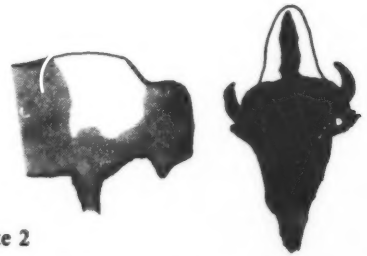
CHARACTER

1 Cape



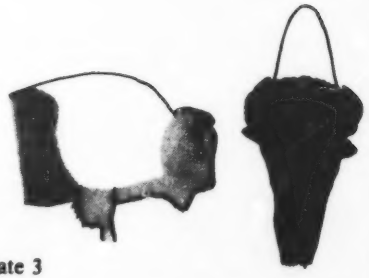
State 1

Colour of cape approximately the same as the rest of the body or dorsally lighter (reddish brown), lighter area up to 25% of cape 0



State 2

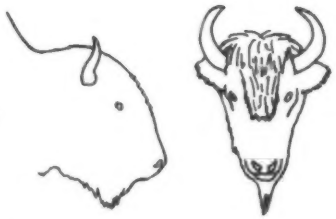
Much lighter than body, light brown to blond, lighter area covering >25% of cape; dark medial line, bisecting lighter areas of cape present 0.5



State 3

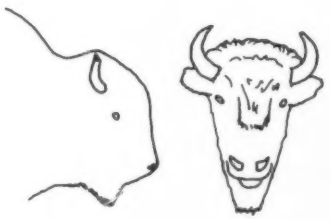
Much lighter than body, light brown to blond covering >25% of cape, dark medial line, absent 1

2 Frontal display hair



State 1

Not well developed, short to moderately long, lying flat forward, often in long strands, not filling space between horns 0



State 2

Denser than in 1, but flat and not filling space between horns; hair on nose may be erect 0.5

State 3

Well developed, long, dense and standing, often forming a "hair roll" between the horns 1

3 Display hair on upper front leg

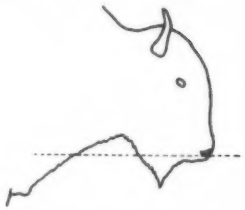
State 1

Short (< 10 cm), not forming distinct "cuffs" or "chaps" 0

State 2

Long forming distinct "cuffs" or "chaps" 1

4 Ventral neck mane



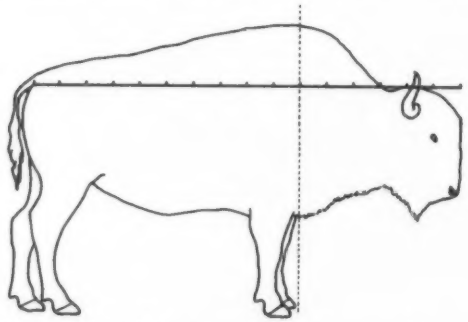
State 1

Little developed in area of neck, behind beard at or above level of nose in normal standing position; beard usually thin and pointed 0

State 2

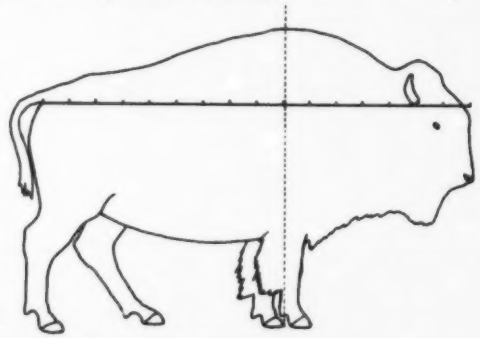
Well developed, in area of neck, behind beard below level of nose in normal standing position; beard usually full and rounded 1

5 Hump



State 1

Highest point of hump anterior, between points 10 and 11, anterior slope to neck precipitous 0



State 2

Highest point of hump posterior, at point 9, anterior slope to neck generally more gradual 1

TOTAL

$\frac{\text{TOTAL}}{5} \times 100 =$ SCORE

B. b. athabascae 0 50 100 *B. b. bison*